

THE AMERICAN NATURALIST

VOL. LXXIII

March-April, 1939

No. 745

THE AMERICAN SOCIETY OF NATURALISTS THE LIFE HISTORY AND PERSONALITY OF THE CHIMPANZEE¹

DR. ROBERT M. YERKES

YALE UNIVERSITY

"In the title 'The mind of a gorilla' you assume what should be proved." This was the critical comment of my colleague, Raymond Dodge, when I proposed so to label an account of the behavior of a mountain gorilla. I replied that "mind" was the best term I could discover for the facts which I had gathered. So likewise in this address I am assuming that personality is the correct and adequate term for what is now known concerning the integrated behavior of the chimpanzee. Indeed, in my present thinking there is no question about the reality of chimpanzee mind, individuality, personality. If you dislike psychological terms, it is your privilege to substitute whatever symbol seems more fitting. I ask only that you acquaint yourself with the essential features of anthropoid behavior before pronouncing my assumption unpragmatic or illogical.

It is my purpose in this address to picture as serviceably as I may in the few minutes allotted me the psychological characteristics of the chimpanzee, to suggest grounds of the animal's peculiar scientific usefulness, and to invite attention to some methodological desiderata which we naturalists are prone to ignore or slight. Speaking primarily from first-hand acquaintance with the

¹ Address of the president of the American Society of Naturalists, Richmond, Virginia, December 30, 1938.

facts, I shall do my best to render a somewhat heterogeneous array of observations meaningful and entertaining. The cinema record from the Yale Laboratories of Primate Biology which will be shown at the end is intended as antidote for boredom.

To put methodological considerations first requires no apology. I should like then to point the contrast between naturalistic and experimental inquiry, since to-day we are assembled as members of an honorable scientific organization whose name directs our thoughts backward and reminds us that many scientists think of the naturalist as having been replaced by the experimentalist. I beg to offer contrary opinion and to maintain that the interests, objectives and methods of the two are supplementary, and neither substitutes nor alternates. For the naturalist, with minimal disturbance of organism or environment, attempts to find out about life as it is lived; while the experimentalist, with some definite problem in mind, seeks so to control the conditions of observation that solution shall be facilitated.

True, the development and application of experimental techniques and skills mark a path of progress toward more exact knowledge and better understanding of animal life and relations. Witness the results of experimental versus naturalistic studies of color vision. But, nevertheless, naturalist and experimentalist may be equally worthy of support, admiration and emulation. Each, it may be argued, is necessary to safely efficient biological advance, since we need to know animals intimately, sympathetically and disinterestedly as natural objects if we are to use them with maximal effectiveness in well-planned experiments. It would be ideal, as I see the situation, if in each of us biologists might be combined the interests and abilities characteristic of the best in field observer and laboratory worker.

Contrasted with rapid progress in the control and measurement of the environmental factors affecting behavior is the relative neglect of the nature and immediate

condition of the animal observed. Continuing in the tradition of the naturalist, the experimentalist too frequently accepts his animal subjects as given in nature and proceeds to use them without adequate knowledge of prior history and immediate condition. Surely it should be unnecessary in this family group to argue for the importance of suitable biological subjects and definite knowledge of their essential characteristics. For it is obvious that in many psychobiological, sociological or more conventionally physiological studies, it is absolutely essential to reliability and interpretability of observations that varied aspects of the life history of the organism—developmental, nutritional, reproductive, disease, experiential—be known. In such case our subjects should be bred in a laboratory colony, reared and maintained under appropriate conditions, and used as relatively standardized observational materials. How amazing, when one pauses to consider it, the difference between the requirements of a chemist relative to the purity, describability and dependability of his materials and those of the physiologist, psychologist or sociologist. In case of self-pity we may claim that ours in varied respects is a more difficult task than is that of the physical scientist, but against this must be placed the admission that one satisfactory organism is likely to be of more value than scores whose special suitability is merely taken for granted. Actually the two are incomparables, as are correct and incorrect observations. It is my earnest plea, therefore, that we pay more heed to the origin, nature and status of our animal subjects and to their immediate fitness for experimental use.

Freed from varied superstitions concerning living things, it is now our opportunity and obligation to strive to shape them in accordance with experimental requirements and on occasion to specification. What a far cry biologically from the naturally given animal to that which is experimentally produced and conditioned as biological test or experimental object. The organism is continuously in flux; varieties and variabilities are omnipresent

and of the utmost importance. Upon them, changes both progressive and retrogressive depend.

It is evident that my mind has turned to the problem of species. I wonder how many of us in this learned company could readily and with certainty identify the three genera of great apes—gorilla, chimpanzee and orang-outan—in all their stages of life history. It is not my present intention to try to inform you about the content and differentia of our own order, the primates. Instead I would inquire humbly, for I am not a taxonomist, whether the terms genus, species and race have the same significance when applied to man or chimpanzee, or if not, why not? We hear commonly about genus *Homo* and genus *Pan*; about races of man and species of chimpanzee. But if species of the latter why not also of man, since human races appear to differ more from one another than do the so-called species of chimpanzee? Have we perchance, in formulating this seemingly naïve question, stumbled upon a persisting biological myth; namely, that man as lord of creation stands unique and incomparable, separated by a vast gulf from the remainder of the organic world? It seems that even in taxonomy we are reluctant to apply to ourselves the rules which we habitually apply to our nearest living kin, the anthropoid apes. But, despite our prejudices and superstitions, truth marches on and wisdom and enlightenment increase with the extension of knowledge. In the Yale Laboratories of Primate Biology, where by the broad-minded liberality of Yale University and the Rockefeller Foundation it is my privilege to work, we are seeking by several routes to cross the gulf between man and anthropoid ape, that we may know ourselves and them in true genetic relation and perspective. By most of the paths progress is slow and halting, but in some directions the fruits of our labors are most encouraging.

My psychobiological knowledge of the primates stirs me to ask also whether the taxonomist may reasonably hope to proceed safely in his revision of the Order Pri-

mates without knowledge of the age, developmental status, normality and degree of typicalness of his specimens. Such taxonomically favorite characters as those of teeth, skeleton, skin, coat, body form, are known to vary with age, nutrition, state of health and other factors. Often this seems to have been ignored by species-makers, and as a result we have descriptions of a score or so of chimpanzee species. Perhaps we are too lenient with ourselves in this field, as well as in our studies of behavior. Certainly times without number specimens have been accepted as they chanced to come to hand, although clearly enough essential information about them was lacking. The argument which I have in mind runs thus: We can not hope to classify animals serviceably without knowledge of age and of those changes which characterize the life cycle. Even taxonomy is bound to natural history.

It is incomparably more illuminating to follow the life history of an animal from birth, or earlier, to maturity than to know it only in cross-section at some particular stage of development. Few biologists unfortunately have had opportunity to follow a chimpanzee through its decade of development. Such rare good fortune, as it has come to me in the past twenty years, together with the invaluable contributions of my associates in primate research, enable me to describe this ape in terms of three series of events: the sexual cycle, the reproductive cycle and the life cycle. Of necessity my account will be synoptic and far from ideally complete, for as yet we are ignorant of much that is important.

The chimpanzee sexual cycle typically occupies five weeks. Menstruation, genital swelling and oestrus are readily observable. Shortly after the completion of menstrual bleeding the genital-anal tissues begin to exhibit tumescence. Within one to three days the area has swollen to surprising proportions. Maximal swelling continues about ten days. In extreme cases the volume has been estimated as four liters. During the period of



genital swelling, and ordinarily only then, the female is sexually acceptable to the male. Her receptivity, and presumably also her sexual desire, appear to wax until a maximum is achieved during the last few days of genital swelling. It is during this interval, according to our observations (Elder, 1938), that ovulation and fertilization occur. Indeed, we have no evidence of conception in any other phase of the sexual cycle than during the last few days of maximal swelling. The human cycle differs notably from that of the chimpanzee in being about one week shorter, in the relative inconspicuousness or absence of genital swelling and oestrus, and in the reported occurrence of conception during other cycle phases than the period to which it appears to be restricted in the chimpanzee.²

By the cooperative functioning of male and female during the appropriate phase of an ovulatory sexual cycle, the latter may be converted into a reproductive cycle. Mating behavior may be initiated by either sex. Female receptivity is indicated to the male by the genital appearance of the female and also by her behavior. Either sex may be dominant. As yet we are ignorant of the life span of the ovum after the rupture of the follicle, and also of that of the spermatozoon in the reproductive tract of the female. Until these facts are reliably established, neither the time of ovulation nor that of conception can be stated with accuracy and certainty. With the possible exception of the Burr electrical variation method (Burr, Lane and Nims, 1936), no conveniently applicable procedure for the observation of ovulation is available.

Ovum implantation, as observed by Carl H. Hartman (Elder, Hartman and Heuser, 1938), is deep in chimpanzee as in man, instead of superficial as in the monkeys which have been studied. This would seem a very significant point of similarity between man and chimpanzee. Probably it will presently be discovered to be common to the anthropoid apes and man.

² Knowledge of human ovulation is still incomplete and observations are difficult to evaluate.

Gestational process from conception to birth requires about thirty-four weeks in chimpanzee, as compared with thirty-eight weeks in man, or approximately eight versus nine months. To judge from our observations, parturition as a rule is neither prolonged nor so difficult as to endanger the condition of mother or infant. Vertex presentation appears to be typical, and so also is placentophagia, either partial or complete.

Normally the infant is accepted by its mother as soon as it emerges from her body, carried about continuously, cleaned with lips and fingers, and finally permitted to cling to her abdomen, groins or breast, except as she handles it for purposes of care or of her own comfort.

Continuing this account of the reproductive cycle into the individual life cycle, we note that after as before birth the rate of physical development in chimpanzee is appreciably more rapid than in man. If body weight be taken as index of growth and development, it is discovered that the curve of growth for the ape is very like that for man, "being characterized," as we have recently been able to report from our anthropometric data, "first by an infantile period (birth to 24 to 30 months) during which the time rate of growth (velocity) gradually decreases; second, by a juvenile period (3 to 7 or 8 years) in which the time rate increases at a constant rate; and third, by a mature period (7 or 8 years to 11 or 12 years) during which the rate of growth gradually decreases to zero. The pattern of the curve of growth of chimpanzee is much more similar to that of man in quantitative and qualitative characteristics than to that of other mammals which have been studied. The major inflection point at the junction of the positively accelerated juvenile period and the negatively accelerated mature period coincides in chimpanzee as in man and other mammals with the physiological stage of puberty. The relative rate of body growth in chimpanzee during the positively accelerated pre-pubertal phase is about 25 per cent. per year as compared with 10 per cent. for man and 1000 per cent. for other mammals

in corresponding periods." (Spence and Yerkes, 1937, pp. 244-245.)

Chimpanzee infancy, as period of relative helplessness and utter dependence upon mother or other older individual, is a brief two years. Whether if left to its own resources in a highly favorable material environment the year-old baby would survive is doubtful. But certainly if it be two or more years advanced, it should be able to do so without special difficulty. Ability to walk, climb, exercise and play about may be achieved by the middle of the first year, and these develop apace during the latter half.

As in us, childhood, with its freedom from cares and responsibilities, is a period of extreme playfulness. It is the period of development which most strongly appeals to men who use these animals as subjects, whereas by contrast, and naturally, the period of infancy is more appealing to women. A more high-spirited, good-natured, responsive, affectionate and entertaining pet than the chimpanzee child is difficult to discover.

But with the onset of adolescence the stream of life tends to run less smoothly, for problems involving the adjustment of the physiological self to environment abound. There are conflicts of interest and desire; evenness of temper and playfulness become less predictable, and at times impatience, irritability or downright meanness may be manifest. To the friendly observer who has been on terms of intimacy with the individual from its birth, this change may be disturbing and question-provoking. It becomes increasingly difficult to get along with the ape, and especially so in the case of the female. As the biologist appraises the situation, the individual is on the threshold of maturity and racial functions have thrown their shadows before.

Sexual maturation requires from seven to ten years. It is attained somewhat more rapidly than by man in the tropics. The duration of the reproductive life of the female ape has not been measured. In our Yale chimpanzee colony there is one female who is still breeding at

an estimated age of twenty-six years. She seems old to us, but not senile. One would surmise that the reproductive period may not ordinarily exceed twenty years in duration. As for the length of life of the chimpanzee, our ignorance is complete. It is indeed a long task to rear a sufficient number of subjects and to follow their histories to death in old age from natural causes. I do not venture a guess as to the average span of life in nature or under favorable conditions of captivity.

It is not without significance for the interpretation of our results that until recently most of the behavioral studies of the chimpanzee have been made on young specimens. Chimpanzees they are to be sure, but how different psychobiologically from their adult selves.

The sexually mature or middle-aged ape, even if still friendly, gentle and cooperative with the observer, is no longer forthright and eager in play, overflowing with the joy of activity, even-tempered and fairly dependable. Instead he or she tends to be grave of mien, quiet, relatively inactive, attentive to the necessities of life, but somewhat impatient of everything else. Serious-mindedness is the most apt phrase. One may not with impunity joke carelessly or thoughtlessly with a really serious-minded acquaintance, whether man or chimpanzee! Beyond the first decade in its life history, chimpanzee playfulness and fooling behavior rapidly diminish until they become very rare. It is not that the individual has become unfriendly or morose; one has instead a sense of the gravity or weightiness of the duties and obligations of being an adult ape, for evidently in growing up they, like ourselves, gradually lose buoyancy and the tendency to be lavish of energy in activity and emotional expression. Aging it is, and by twenty years this primate ordinarily is as old behaviorally, and perhaps we can safely say psychobiologically, as we are at forty to fifty years. How fascinating and bewildering are the changes in attitude and activity from birth to maturity. It is to be hoped that some time we shall be able to record cinematographically

this varied series of anthropoid events, condensing a decade of development into an hour of observation.

At the moment I am unable to complete this thumb-nail sketch of chimpanzee life history by including the characterization of senility, since it has not been our good fortune to observe any individual in this phase of life. The oldest of my acquaintances are in their third decade, with no definite indication that they may not live for many years.

As Köhler has aptly said, "It is hardly an exaggeration to say that a chimpanzee kept in solitude is not a real chimpanzee at all" (1925, p. 293). It has become perfectly clear that only in a favorable social environment does the personality of this ape emerge and develop normally. It is for this reason that I now turn to the facts of social behavior and relations for material to complete this picture of chimpanzee life.

Behavioral development in the ape is from initial social dependence to dominance; from clinging or clasping to venturesome climbing and independent bread-winning. In the early months of postnatal existence the infant securely grasps the mother and is carried everywhere with her. Maternal care preserves and safeguards it, and both early and late maternal example and tuition facilitate habit-acquisition and adaptation to many types of problem situation. To a degree which it would be difficult to overestimate, the female of the species shapes the development of the individual. Indeed, it is not until childhood that the little chimpanzee escapes the surveillance of its mother, dares to face the unexpected and startling events of its world and to live abundantly in the company of its juvenile peers. Thenceforth and increasingly, child learns from child, and social contacts become more varied and exciting, if not more exacting as well. The playful personality speedily emerges, together with those social behavior patterns which later will determine the place and relations of the individual in the social order.

The behavior which the term dominance usefully desig-

nates is manifest during childhood, takes more definite form in adolescence, and hardens into habitual forms of expression in maturity. Ultimately, by its dominance-subordination attitude and behavior, the individual establishes its place in the social hierarchy. It may command the right to have its own way with its fellows in any situation, to impose its will and desire on the group no matter how unfair or inimical they may be to immediate social welfare; or, on the contrary, it may meekly accept a subordinate place and in a sense become enslaved. For in its extreme expression, dominance spells selfishness, injustice, tyranny, cruelty. The contrast between dominant and subordinate chimpanzee personalities is rich in significance for students of social science.

By virtue of hereditary constitution, as modified by individual experience, there appear two types of ape personality: the one constituted to command, and the other content to obey. To the former fall inevitably opportunities and demands for leadership, initiative, adventure, progressiveness and varieties of social service; and to the latter, the opportunity or necessity to follow, serve, consolidate advances. In our genus we think of the male as typifying dominance, and the female, subordination. Yet we know, from available facts, that the situation is by no means so simple and the dichotomy far from true. It is even clearer for the genus *Pan* that an individual, irrespective of sex, may be dominant and domineering or the opposite. In general, might makes for right in chimpanzee life, but physical prowess may be outmatched by intelligence, courage and self-confidence.

Physique, intelligence, temperament and experience, as objectively evaluated and describable in behavioral terms, stand forth as the essential determining conditions of those social behavior patterns which we have come to designate as dominance and subordination. Highly impressive and socially significant in ape as in man are such biological contrasts as robust and puny, bright and dull, well-adapted and inept, courageous and cowardly.

Even a hasty, incomplete sketch of the psychobiological characteristics of the chimpanzee must include such likenesses and unlikenesses to man as the following. The modes of sense, so far as known, are the same in ape and man, and so also the order of keenness and range in each. Perceptual processes, although relatively little known, evidently differ markedly in the two primate types in correspondence with differences in their manner of life as well as their physique. Undoubtedly there offers engaging opportunity for discovery in this psychobiological sphere, for without knowledge of its perceptual capacity it is difficult to imagine or predict the behavioral adjustments of an organism. As to memory, the chimpanzee is efficiently equipped, for it remembers well and long anything which vividly impresses it. Analyses with respect to memory content, detail and accuracy await future investigators. By contrast with memory as reproduction or revival of psycho-neurological processes, imagination, although frequently evidenced by the behavior of the ape, is of relatively low order, simple and incomparably less important than in man. Were this type of creative process more common, the animals might be expected to develop a spoken language. As a fact, they depend for intercommunication primarily on bodily posture, gestures and sounds; and of language as a system of symbols used serviceably for the expression of experience, they have none. It appears that man as thinking and talking animal is virtually unique. There are evidences in the life of the chimpanzee of what in ourselves we term ideational processes, insight and reasoning, but they are relatively infrequent, and at a stage of development and functional usefulness which suggests human infancy or early childhood. Perhaps more than in any other sphere, this ape resembles man psychobiologically with respect to its modes of affective expression. That it feels as we do may not be asserted with assurance, but it is clear that under conditions which affect us emotionally it manifests similar expressions.

A few additional glimpses of the chimpanzee personality as it functions in social situations should appear as high lights in the picture.

With a facility which from late infancy to maturity steadily lessens, these apes acquire attachments to one another and to human acquaintances. Particularly in face of such imperative needs of social service as in illness, injury, threat to safety or inability to meet a baffling situation, positive affective bonds give expression to gratitude, sympathy and fondness. One is not often left long in doubt about the attitude of the animal, for attractions or aversions tend to make themselves felt almost immediately: the former in pleasant or even flattering ways, the latter by actions which may be repelling or belittling. Along with many weak and transient attachments there are some which endure for months, years or perhaps even throughout life. It is no over-statement to assert that chimpanzee friendship or enmity for fellow ape or man may be exceedingly strong and permanent. Teasing, unfair or unkind treatment may almost instantly establish hostility and antagonism, whereas the opposite in treatment may induce appreciative friendliness. The significance of these facts for the social life of chimpanzees and the guidance of persons who care for or use them is too evident for comment.

It is a primary task of caretaker or experimenter to win the confidence and trust of his subjects. Affective attachment implies a measure of liking and of dependence, but not necessarily confidence. The latter is achieved, if at all, through patient, tactful and understanding treatment of the chimpanzee subject. To attempt to command or to hasten its acquisition is likely to be fatal to success. Individual differences in the granting and also in the depth of confidence are extreme. Some individuals grant it readily and completely, others not at all. Likewise some persons with facility command the trust of their ape subjects, while others have extreme difficulty in doing so. Ordinarily trust, whether among apes or between ape and man,

becomes mutual and establishes or reenforces attachment. This is the secure basis of success, facility and safety in handling the animals, whether as pets, stage performers or experimental subjects.

Confidence is also the essential basis of cooperation. Once an investigator has won the complete trust of his subject and its affection, he may count on obedience and cooperation to extraordinary lengths. To this end it is necessary only that he make the animal understand what he wishes, control and direct its interest, and free it from inhibiting fears. Under these conditions even irksome, distasteful or painful experiments may be conducted with the wholly voluntary cooperation of the trained and experienced chimpanzee. The concluding phrase is important, for unless previous experience has acquainted the animal with what is required of it in the experiment and with what may be expected to happen, it is likely to be timid and apprehensive, despite its friendliness toward the experimenter and its confidence in him.

Whereas formerly most of our exacting behavioral studies in the Yale Laboratories of Primate Biology were conducted under conditions of subject-confinement, restraint or coercion, more intimate acquaintance with the characteristics of our subjects and extended experience have taught us that in many instances voluntary cooperation of the free subject may be relied upon. This is an important discovery in methodology, for in not a few of our investigations coercion or force is unfavorable to the reliability and interpretability of results, and in all cases cooperation without restraint makes for safety, convenience and economy of experimental effort. In a word, then, attachment, mutual confidence, familiarity with the situation, freedom from intruding fears and willingness to cooperate on request or command, pave the road to success in most varied and exacting experimental quests.

Intimations of altruism may be discovered in the behavior of many mammals, but the evidences are most varied and abundant in the life of anthropoid apes and

man. Functionally viewed, an act of fellow service may be more or less unselfish, but it is doubtful that any act, even in man, is purely altruistic. It happens that "grooming" is a pattern of chimpanzee behavior which at times supplies convincing examples of social service. A simple form of this activity is familiar to all visitors to the zoo as flea-picking. For many types of monkey in captivity this is a favorite pastime. It may be mutual or self-directed, but in either case it is usually a toilet-making process instead of a search for ectoparasites. The chimpanzee grooms self or companion with skill and evident enjoyment. Lips, teeth and hands may be employed, and as the activity proceeds sounds frequently are made with tongue, teeth and lips. The behavior is not necessarily correlated with sex. It is rare during childhood, more frequent in adolescence and characteristic of the sexually mature individual, who may groom another individual irrespective of age. Often grooming is solicited, begged for, insisted upon or commanded, in accordance with the dominance-subordination relation of the individuals. This frequently appearing behavior pattern serves to keep the skin and coat clean and neat, to remove thorns, splinters, burs, chiggers, to cleanse or drain surface wounds or abscesses. Obviously such service is especially important for regions of the body inaccessible to the individual. Grooming often is necessarily a vicarious service, and whether willingly and eagerly or reluctantly performed by the groomer it constitutes social service and in so far may be considered altruistic. Chimpanzee fellow-service is not limited to grooming. I have selected this behavior from among many varieties merely for illustrative use.

If the impression has been given that the personality of chimpanzee is relatively uniform and constant, violence has been done to the facts, for there are individual patterns and types. One may as readily identify a familiar ape among many by its personality as mirrored in behavior as by its physical appearance. The student comes soon to recognize his subjects as in varying degrees pa-

tient, tractable, docile, suggestible, gentle, friendly, trustworthy or the opposite. There are preferred and neglected individuals in any group of experimental chimpanzees, for one may quickly grasp the requirements of a situation, cooperate perfectly and facilitate the work of the investigator, whereas another may be slow, unpredictable, relatively uncooperative or even refractory. There are good and ill-natured individuals, stable and unstable, calm and excitable, industrious and lazy.

Because amidst important differences the chimpanzee is incomparably similar to man in structure, development, physiological processes, behavior, social relations, susceptibility to disease, response to various educative or therapeutic measures, it should prove invaluable to science. Naturalistically viewed, it is a fascinating object, knowledge of which, although growing slowly for decades, is still fragmentary and sadly inadequate to the needs of investigators. Experimentally considered it stands as unique in potential availability, controllability and usefulness for attack on many problems of psychobiology, sociology and experimental medicine, to mention only a few areas of interest. The exploitation of this extraordinary resource for biological progress lags because of lack of interest, faith and material resources.

It is not by oversight that I have neglected to use observations and contented myself with description in general terms, for I count upon the cinema record which you are about to see to lend reality to my subject. Moreover, I have avoided what might seem like behavioral incident or anecdote.

LITERATURE CITED

- Burr, H. S., Lane, C. T., and Nims, L. F.
1936. *Yale Jour. Biol. Med.*, 9: 65-76.
Elder, James H.
1938. *Yale Jour. Biol. Med.*, 10: 347-364.
Elder, J. H., Hartman, Carl G., and Heuser, C. H.
1938. *Jour. Amer. Med. Assn.*, 111: 1156-1159.
Köhler, Wolfgang.
1925. "The Mentality of Apes." Pp. viii + 342. New York.
Spence, Kenneth W., and Yerkes, Robert M.
1937. *Amer. Jour. Phys. Anthropol.*, 22: 229-246.

THE EXPERIMENTAL ANIMAL FROM THE NATURALIST'S POINT OF VIEW¹

DR. G. K. NOBLE

AMERICAN MUSEUM OF NATURAL HISTORY

THE naturalist is popularly supposed to be one who studies animals or plants under natural conditions. To-day there is an increasing group of naturalists who are concerning themselves with the productivity of natural populations and its bearing on forest, fish or game management. These workers have shown that wild populations are in a continuous state of change, that the balance of nature is usually unbalanced. In addition to the changing predator-prey relation and the cover-carrying capacity correlations (Errington, 1937) there are less tangible social integrations to consider. Langlois (1934) has showed that the black bass, *Micropterus dolomieu*, for example, can be reared more successfully in clear ponds free of vegetation and provided with artificial foods than under conditions which appear to be much more natural. "The occurrence of superiority and awareness of it, and of inferiority and awareness of it, in the case of bass leads to cannibalism," Langlois states, and to grow large bass crops one should adopt measures to make the fish more socially minded.

The principles of social integration in fish should be of interest to others besides fish culturists. Endocrinologists have described numerous sexual differences among fish, some under nervous control but others regulated by sex or pituitary hormones. The functional significance of these differences can be determined only by reference to the social life of the fish. Again, recent discoveries in paleontology have tended to bridge the gap between the classes of vertebrates. We can now trace with consider-

¹ Read at a Symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America and Section H, The American Association for the Advancement of Science, Richmond, Virginia, December 30, 1938.

able assurance the changes in the skull from fish to man. Although man is equipped with certain special endowments not found in other vertebrates, he is nevertheless a social animal and we may well ask where in this series did his social behavior first arise. If it should be possible to trace the components of his social behavior to their beginning in lower vertebrates, the next question is, What are the mechanisms responsible for this behavior?

A school of fish is held together by innate attractions. This is readily shown by rearing aquarium fishes (such as *Hemichromis bimaculatus*, etc.) from a very early age in isolation.² When placed in a tank with several species they will eventually school with their own kind (Noble and Curtis, 1939). Fish reared singly with other species also school with their own kind when given the opportunity. The size of the species concerned, the manner of swimming, the reaction of the resident fish modify the result, but basically there is a species attraction, as Picard (1933) assumed. Blinded aquarium fish school very feebly, if at all, and hence vision would seem to be the chief sense modality mediating schooling. Nevertheless, fish may not be attracted by an inborn image of their own species. Fish tend to move towards other moving objects and to react under different conditions in ways peculiar to their own species. The guppy, *Lebistes reticulatus*, for example, when seriously disturbed, moves against gravity and hence the group tends to aggregate near the surface of the water. Young catfish, *Ameiurus melas*, although attracted by motion, are also stimulated by contacts with their own kind, but whether this is a conditioned response has not been determined (Bowen, 1931). In some cichlids there seems to be an inborn attraction to particular motions. *Hemichromis bimaculatus*, isolated at only 5 days of age and reared for 77 days with *Cichlasoma cutteri*, returned at once to their own species when given the opportunity (Noble and Curtis, 1939).

Directly opposed to this cohesive force of the group

² This investigation was supported in part by a grant from the National Research Council, Committee for Research in Problems of Sex, and in part by a fund from the Josiah Macy, Jr. Foundation.

attraction, there is in most aquarium fishes, and presumably in teleosts in general, a continuous aversion for one another which expresses itself in a dominance drive. Every fish by threat or blow seeks to gain dominance over every other member of the school. There results early in life in such fish as *Xiphophorus helleri* a straight-line "pecking order," similar to that which has been described for the domestic fowl (Schjelderup-Ebbe, 1924). Fish near the top of the order have better access to food and mates (Noble and Borne, 1938). During periods of starvation, fish at the top of the order lose less weight. Large or heavy fish tend to dominate the others, but there are many factors which may give the advantage to a lighter fish. Mere familiarity with an area gives the resident a decided advantage over a newcomer. The former usually attacks first and, if there is not too great a discrepancy in weight, it will become dominant. Brighter or more energetic fish usually dominate. Merely cutting the sword from the tail of a male *X. helleri* usually drops him in the dominance hierarchy, but after a time he may regain his position by fighting. The order in a small school may remain constant for two or three weeks. Female *X. helleri* following parturition usually rise in the order. Dominant fish do not permit subordinates to fight near them without seeking to "punish" them. Apparently the gestures of the aggressive subordinate stimulate the dominant fish to exert its authority. Usually the fish second in order receives more blows from the despot than the one third in order, and the latter more than the one fourth in order, etc., but under certain conditions a fish low in the order may evoke the attacks of the despot far more than do the fish higher in the social order. Every fish in the school seems to know every other as an individual, and every subordinate appears to be awaiting an opportunity to revolt against the despot. An attack upon a despot frequently leads to a complete revolution within the group, each individual taking up a new position in the order.

At sexual maturity the dominance hierarchies are dis-

rupted by the sex drive of the males. Female *Xiphophorus* may still retain their straight-line order, but at that time even relatively small males will attack them. There results a new order with the females confining their blows to females, and the males to their own sex. This "chivalry" is not due merely to the greater strength of the males, for castrated males usually resume their attacks. Mature males would seem to have a latent sex interest, which becomes manifest in overt behavior only at intervals, and this keeps the dominance drive against females in check. The secondary sexual characters of the male serve to identify his sex, for if a small female has a sword artificially attached to her tail she is treated like a male by the other fish. Conversely, a male with his sword and gonopodium removed is treated like a female (Noble, 1938).

In nest-building fish, such as *Hemichromis bimaculatus*, the young when free of their parents establish straight-line dominance hierarchies regardless of sex (Noble and Borne, unpublished). At sexual maturity these hierarchies are modified in a manner different from that in the live-bearer, *Xiphophorus*. The breeding fish, usually the male, claims a territory containing a suitable spawning area and drives off other fish from this region. A subordinate male with territory becomes dominant over his despot and over other males which enter this area. Gravid females, attracted by the male's display and symbolic nesting movements, enter his territory. If two males are available, the female is attracted by the more conspicuous fish (Noble and Curtis, 1939). In other words, there is a true sexual selection in the sense of female choice. The courtship movements of the female *H. bimaculatus* are also stimulating to the male and her threatening gestures ward off predators from her eggs and young. It is therefore not surprising that the female as well as the male becomes conspicuous by an expansion of erythrophores during the breeding season.

Since all birds are egg-layers, the territorial habit is

well developed in this group. The territories, however, may be very extensive and have the secondary function of assuring an available food supply for the young. In many primitive birds, such as the night heron, the territories retain their piscine function of being primarily a place where sexual bonds may be formed. These are necessary in both fish and bird if the mates are to be held together as a pair during the breeding season (Noble, Wurm and Schmidt, 1938).

Fish which school more than *Xiphophorus* or *Hemichromis* are unable to maintain the straight-line hierarchies of these forms. Instead, as in *Barbus partipentazona* and *Danio malabaricus*, each despot may receive some blows in return from its subordinates. There results a peck-dominance system similar to that Masure and Allee (1934) described for the pigeon. This apparent confusion of hierarchies seems to result from the more compact groupings of these better schooling fishes and better flocking birds. At least in forms where the species attraction seems to be poorly developed, the dominance hierarchies tend to be better established. An exception occurs in the case of *Betta splendens*; the females develop straight-line systems, but the males are so aggressive that no true order is established. Dominance behavior has apparently a genetic basis. At least the white strain reared in our laboratory in the same tanks as colored varieties proved inferior to them even when greatly exceeding them in weight.

Dominance hierarchies, although well developed and of several types in fish, never reach the complexity found in higher forms. Weight becomes in these higher vertebrates of less importance than other factors in helping an individual secure dominancy. Many birds and mammals recognize not only the individual but the group. Resident hens when confronted by a group of newcomers distinguish the new hens from their own group (Skard, 1937). Jackdaws are also able to keep the group in mind, acting as a group against intruders of their own species

(Lorenz, 1931). No fishes apparently react as a group towards newcomers. In *Xiphophorus*, either a single newcomer, if sufficiently large, or a group of new fish will produce a revolution in the resident hierarchy. In the latter case each fish fights for itself against residents and introduced individuals. While the dominant resident usually remains the despot, a fish from either group may rise to second place in the order.

Although mammals, like fish, exhibit a variety of dominance hierarchies, a marked advance is found among certain forms especially the anthropoids (Yerkes, 1934). In the chimpanzee, subordinates are attracted to dominant individuals and frequently imitate them. Wheeler (1930) assumed that the dominance drive was a cohesive force in vertebrate sociology. At the fish and bird level it is exactly the opposite. Murchison (1935) described the hen as being attracted by the more dominant rooster. This, however, seems to have been a sexual attraction similar to that shown by the territory-seeking *Hemichromis* female. Dominance behavior in fish and birds begins long before sexual maturity and tends to keep individuals at a distance. Were it not for the cohesive group attraction, it would completely destroy the group.

The cohesive force in fish society seems primarily innate, although the influence of training may be in some cases readily demonstrated. In birds, training plays a much greater role, many species form sentiments about others (Bannister, 1932) and acquire social companions among them (Lorenz, 1937). A short exposure of the gray-lag goose at the time of hatching to an observer may cause the goslings to follow him (Heinroth and Heinroth, 1928). Hence, the stimuli calling forth the "herd instinct" may be in one species innate and in another learned. Cowbirds which return to their own flocks after being reared by foster parents apparently have an innate species attraction. In mammals, also, learned or unlearned incentives, such as species odors, may produce the adequate stimulus for calling forth the herd response. In

domestic mammals, such as dogs, the innate attraction may be reduced to a minimum.

The elaborate development of the voice in birds formed an important advance in vertebrate phylogeny. Already at the frog level, voice had important functions both in attracting females and repulsing males (Noble, 1931). It could be used also to warn companions or frighten enemies. But frogs never developed the variety of meaning to their calls found in birds. Suggestive movements more than sounds regulate the social life of fish. They control the movements of the school and correlate the feeding activity of the group (Welty, 1934). The courtship behavior of the female *Hemichromis bimaculatus* will call forth similar behavior in the male (Noble and Kumpf, 1936). When the European minnow, *Phoxinus*, is aroused by the odor of its own cut skin, it dashes away in fright, and this state is apparently transmitted by the rapid escape movements to other members of the school, even if they have not sensed the odor (von Frisch, 1938). In *Tilapia macrocephala*, the same reaction occurs but only in juvenile fish. In birds, movement, posture and especially voice play an infinitely greater role in correlating the activities of the group. If a gull stretches its neck in a particular manner or a duck moves its head in a special way, the other members of the flock prepare at once to fly. Moods are rapidly spread throughout the group by an expressive attitude of any one individual (Lorenz, 1935; Tinbergen, 1936). Some fish, such as *Hemichromis*, brood their eggs and call their young to them with distinctive fin gestures. Further rapid movements of the parents may cause the young to flee. The control of the behavior of young birds by specific cries of their parents was an important advance in vertebrate phylogeny. It made possible greater protection for the young during this critical period of their life history.

In brief, while in the evolution of vertebrates there has been a great improvement in social behavior, at the fish level at least four of the principal components of social

life found in the highest vertebrates had already developed: (1) group attraction, (2) dominance-subordination behavior, (3) suggestion, and (4) parental service. In each of the three classes: fish, birds and mammals, great variation in some of these components occurs. Peck right has repeatedly changed to peck dominance, and parental behavior has dwindled or disappeared. But where these elements of social behavior occur, they are readily recognized in spite of improvement or degeneration.

In view of the repeated occurrence of these elements in different classes of vertebrates, the question remains, are the neural mechanisms responsible for these types of behavior the same in all vertebrates? If we remove the forebrain of a teleost, such as *Hemichromis bimaculatus*, it feeds and swims perfectly, but it can not follow a school (Noble, 1936). This is due to its inability to follow the school in its rapid turnings throughout the tank. The inability of fish to take a variable path may be accurately measured by testing it in a maze. An effective type is an opaque maze with a long path leading from the starting chamber directly to an outer chamber of the tank and arranged with a series of side boxes leading off either side of the central corridor. Intact fish when familiar with the maze will invariably explore the side compartments. No food need be given, since adequate motivation is the tendency of fish to escape from an enclosed space into a better lighted aquarium. *Danio malabaricus* with a mere rudiment of the forebrain remaining differ markedly from the controls in dashing straight down the corridor or at least showing very little tendency to explore. By testing a series of *D. malabaricus* with various forebrain lesions, it was found by Noble and Levin (unpublished) that an area in the caudal third of the corpus striatum was required if the fish were to enter many side boxes. It is this area of the forebrain which is required if the fish are to maintain their schools.

Large lesions in the rostral half of the corpus striatum of *Danio malabaricus* had no effect on the schooling abil-

ity, nor, in *Xiphophorus helleri*, on the dominance-subordination relation of the fish. But deep lesions in the caudal half of the corpus striatum caused a complete loss of all dominance behavior of the species tested. Male *Xiphophorus* with this area destroyed could mate but only when suddenly confronted by a female. In competition even with much smaller males they were at a decided disadvantage. *Hemichromis bimaculatus* with the caudal fifth of the corpus striatum intact can lay or fertilize eggs, but courtship and brooding movements are either entirely absent or very defective. Hence, in both *Xiphophorus* and *Hemichromis* the social relations require that the caudal part of the corpus striatum be present.

It was interesting to find that female *Hemichromis bimaculatus* with broad but shallow lesions of the dorsal surface of the corpus striatum were sometimes able to synchronize with the male during courtship and egg laying but never succeeded in cooperating in the care of the young. The females could not resist attacking other fish, even their mates, which came near their young. This condition persisted throughout the life of the fish. In the best case this was 19 months after the operation. During this period the fish bred 12 times and showed the same defect at each spawning (Noble, 1937). In another group of cichlids (*Heterogramma*, *Apistogramma* and *Nannacara*), the female normally drives the male from the eggs after fertilization. Hence the unbalance caused by superficial lesions of the corpus striatum in one group of cichlids produced a result very similar to the normal pattern in another group.

This does not mean that the operations had changed the brain of *Hemichromis* to resemble that of the dwarf cichlids. The total social pattern is not the mere sum of a number of simpler reflexes but is a new organization with properties and rules inherent in itself. Disturbing the balance by surgical procedures may produce new rules, which in this case were similar to those in another group of fishes. These rules were the same in spite of the fact

that the neural mechanisms available in the brains concerned were very different.

Fish and pigeon, although far removed from one another in the phylogenetic scale, agree in requiring the dorsal portion of the corpus striatum (hyperstriatum of pigeons) for successful integration of the mating and brooding reactions (Rogers, 1922). The movements of spawning may be retained in fish after loss of this area and some of the movements of courtship are present in male pigeons after deeper lesions. Pigeons and other birds differ remarkably from fish, however, in requiring the basal part of the forebrain for independent feeding behavior.

In the mammal, removal of the cortex, a structure not found in teleosts, apparently destroys the dominance behavior. At least Winslow (1938) has described such behavior in laboratory cats, and the behavior of the decorticate cat described by Bard (1934) indicated that it was not respecting the rules of such cat society. In the rat, lesions of the cortex reduce the variability of path selection as measured in a maze (Krechevsky, 1937). Large cortical lesions also disrupt the parental behavior of the rat (Beach, 1937, 1938; Stone, 1938) and also the mating behavior of the male of this species (Lashley, 1938). The rat resembles such viviparous fish as *Xiphophorus* in that the male directs his sex behavior towards both sexes and even other species at puberty (Stone, 1922). Sex recognition in *Xiphophorus* is a matter of learning the color and form of the adequate sex partner. In the rat, it seems that the darting movements of the estrous female are learned in the same manner. In the rabbit, where these cues to sex recognition are not available, apparently olfactory cues are combined with tactile and other sensory data to identify the adequate partner. At least rabbits with cortex removed but still retaining their olfactory tracts are able to copulate (Brooks, 1937). Since the female is the more passive partner, destruction of the olfactory bulbs as well as the cortex fails to destroy her mating

behavior. In brief, in those mammals where the male identifies the opposite sex by its distinctive movements, the destruction of the cortex leads to failure to mate. In birds and fishes, it is the destruction of deeper parts of the forebrain which has this result.

The neural mechanisms which regulate social behavior may be activated by fewer kinds of stimulations than normally activate them. A *Hemichromis* female may identify the sex of another fish of her own species when in an adjacent tank and become paired with it. A male pigeon, isolated from his mate, will produce pigeon milk if he can see her brooding (Patel, 1936). Normally, tactile and other sense modalities function in these social situations. Defects of behavior following lesions of the forebrain are not due to losses in either the sensory or motor systems, but to a disorganization of the neural mechanisms responsible for the behavior. The mechanisms of sexual and parental behavior have periodically their thresholds lowered by hormones. Nevertheless, parental behavior may be produced in fish without hormonal stimulation (Noble, Kumpf and Billings, 1938) and the same is true of mice (Leblond, 1937). If the mechanism is destroyed by removing particular areas of the forebrain, hormones are ineffectual in producing the response.

It is clear from the experiments indicated above that there has been a shift of the brain centers necessary for the adjustment between two or more individuals of a social group, from the corpus striatum of fish and birds to the cortex of mammals. Social drives, such as those of dominance, sexual and parental behavior, are the expressions of the activity of these specific mechanisms (Lashley, 1938). Although the organization of these mechanisms is very inadequately known, the operative work indicates that they have changed their locus in the forebrain during the evolution of the vertebrates. The location of the chief mechanisms of social behavior in the cortex of mammals is correlated with increasing importance of this organ of association in the life of mammals. With the

elaboration of the cortex in the primates, there followed other improvements in social behavior. Tradition became more important than in lower forms and insight into the benefits of cooperation formed an important advance. Many of the old components of social behavior, such as that of dominance, were greatly modified (Maslow, 1937). It is these improved components of social integration that form the basis of human society.

SUMMARY

There has been an evolution of the social organization of vertebrates from fish to man. Nevertheless, throughout this series the same components of social behavior may be recognized: (1) group attraction, (2) dominance behavior, (3) parental behavior and (4) suggestion. An improvement in the social organization has included: (1) a change from inborn species attraction to a learned group attraction, (2) from a dominance behavior, recognizing only the individual, to one recognizing groups, and (3) from a subordinate, that considers the dominant individual only as a despot, to one that considers the latter a protector and guide. At the fish level the mood of a member of a social group may be quickly transmitted by the character of the individual's movement to other members of the group. Among higher vertebrates these movements are supplemented by vocal expressions which have specific effects upon the behavior of individuals in the group. In the absence of the forebrain, no social behavior is complete in any vertebrate. Forebrain mechanisms essential for social behavior have shifted from the corpus striatum of fish and birds to the cortex of mammals. The elaboration of the cortex in the higher primates is correlated with an increase in the importance of tradition and insight in regulating social behavior.

LITERATURE CITED

- Bannister, H.
1932. *Brit. Jour. Psychol.*, 22: 242-249.
Bard, P.
1934. *Psychol. Rev.*, 41: 302-329; 424-449.

- Beach, F. A., Jr.
 1937. *Jour. Comp. Psychol.*, 24: 393-439.
 1938. *Jour. Genet. Psychol.*, 53: 109-148.
- Bowen, E. S.
 1931. *Ecol. Monogr.*, 1: 1-35.
- Brooks, C. McC.
 1937. *Am. Jour. Physiol.*, 120: 544-553.
- Errington, P. L.
 1937. *Smithsonian Rept. for 1936*: 243-252.
- Frisch, K. v.
 1938. *Die Naturwiss.*, 26: 601-606.
- Heinroth, O., and M. Heinroth
 1928. "Die Vögel Mitteleuropas." III. Berlin.
- Krechevsky, I.
 1937. *J. Comp. Psychol.*, 23: 139-163.
- Langlois, T. H.
 1934. *Trans. Am. Fish. Soc.*, 64: 146-150.
- Lashley, K. S.
 1938. *Psychol. Rev.*, 45: 445-471.
- Leblond, C. P.
 1937. *Rev. Fr. Endocrinol.*, 15: 457-475.
- Lorenz, K.
 1931. *Jour. Ornith.*, 79: 67-127.
 1935. *Jour. Ornith.*, 83: 137-213; 289-413.
 1937. *Auk*, 54: 245-273.
- Maslow, A. H.
 1937. *Psychol. Rev.*, 44: 404-429.
- Masure, R. H., and W. C. Allee
 1934. *Auk*, 51: 306-327.
- Murchison, C.
 1935. *Jour. Soc. Psychol.*, 6: 3-30.
- Noble, G. K.
 1931. "The Biology of the Amphibia." New York and London.
 1936. *Anat. Rec.*, 64: Suppl. 3: 34.
 1937. *Anat. Rec.*, 70: Suppl. 1: 58.
 1938. *Biol. Rev.*, 13: 133-158.
- Noble, G. K., and R. Borne
 1938. *Bull. Ecol. Soc. Amer.*, 19(2): 14.
- Noble, G. K., and B. Curtis
 1939. *Bull. Amer. Mus. Nat. Hist.* (in press).
- Noble, G. K., and K. F. Kumpf
 1936. *Anat. Rec.*, 67(1): Suppl. 1: 113.
- Noble, G. K., K. F. Kumpf and V. N. Billings
 1938. *Endocrinol.*, 23: 353-359.
- Noble, G. K., M. Wurm and A. Schmidt
 1938. *Auk*, 55: 7-40.
- Patel, M. D.
 1936. *Physiol. Zool.*, 9: 129-152.

- Picard, F.
1933. "Les phénomènes sociaux chez les animaux." Paris.
- Rogers, F. T.
1922. *Jour. Comp. Neurol.*, 35: 21-60.
- Schjelderup-Ebbe, T.
1924. *Zeits. Psychol.*, Leipzig, I Abt., 95: 36-84.
- Skard, A. G.
1937. *Acta Psychol.*, 2: 175-232.
- Stone, C. P.
1922. *Jour. Comp. Psychol.*, 2: 95-153.
1938. *Jour. Comp. Psychol.*, 26: 217-236.
- Tinbergen, N.
1936. *De Levende Natuur*, 40: 262-280.
- Welty, J. C.
1934. *Physiol. Zool.*, 7: 85-128.
- Wheeler, W. M.
1930. "Societal Evolution," "Human Biology and Racial Welfare,"
by E. V. Cowdry, New York.
- Winslow, C. N.
1938. *Jour. Genet. Psychol.*, 52: 425-428.
- Yerkes, R. M.
1934. *Jour. Soc. Psychol.*, 5: 271-282.

SOME CONTRIBUTIONS OF THE LABORATORY RODENTS TO OUR UNDERSTANDING OF HUMAN BIOLOGY¹

DR. C. C. LITTLE

R. B. JACKSON MEMORIAL LABORATORY, BAR HARBOR, MAINE

I.

IN the halcyon days some thirty years ago when the small group of then existing experimental mammal geneticists was intellectually drunk on the bock beer of newly rediscovered Mendelism, the idea of such a topic as that which I am to discuss would not even have entered the genially bewildered heads of a program committee.

It takes the sobering effects of a huge mass of scrambled literature extending over three decades to make biologists begin to consider the possible debt which they, and the generation which they represent, owe to any given type of material. Only after having filled the avid maw of research workers faithfully and well for a long time is the lowly plant or animal given a partnership right to have its name included on the titular signboard of a general paper in a symposium of this sort.

However, to one who still enjoys titillating his long abused and ample nostrils with the more than ebb-tidal aroma of the rodent laboratory, and who still thrills at filling his increasingly carcinophilic lungs with the rat and rabbit-ridden, guinea pig-glutted and mouse-muddled air of that enlivening environment, the challenge of presenting such a paper is a welcome one.

It is amazing how effectively experimental work with laboratory rodents has shaped the development of our whole concept of human biology.

The influence of the comparative point of view has nowhere been more consistent and important in providing

¹ Read at a Symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America and Section H. The American Association for the Advancement of Science, Richmond, Virginia, December 30, 1938.

both a check to too much exuberance and a stimulus to lagging initiative, than in that field.

Let us see, then, whether we can assemble and classify certain facts and impressions bearing on this question in such a way as to help us to evaluate what we already owe and may in the future continue to expect from our scented servants, the laboratory rodents, whose parasites, intestinal and pulmonary infections, abortions and "snuffles" have given us care and sorrow along the road.

We may begin by a brief and admittedly much condensed reference to some of the direct and long-standing contributions which laboratory rodents have made to our knowledge of human biology by serving as invaluable test animals in bacteriology, serology and other phases of experimental medicine as well as in biochemical studies, especially with vitamins and hormones.

Cases of this sort are myriad. To attempt to list them would serve no useful purpose. It is, however, interesting to note that there is more than one way in which the relationship between the human phase of the problem and its laboratory investigation has expressed itself.

There is, for example, the directly comparable situation in which there exists close similarity or identity between the substance studied in rodents and in man. To this group belong the vitamins and hormones. Here the observed results of excess or deficiency are usually directly transferable from the laboratory rodent to man.

Really belonging to this general group also are such procedures as the Friedmann and Aschheim-Zondek tests for pregnancy, although the physiological condition of the human being involved is detectable by the stimulation of a quite different physiological response in the rodent.

Then there is a less direct but still relatively simple relationship in which some microorganism or virus is transferred from man, where it naturally occurs, to rodent material with consistent and predictable effect upon the latter. The studies with yellow fever, syphilis, influenza and pneumonia are cases in point.

In both of these groups there has come during recent years a realization that the genetic nature of the rodent material was an extremely important factor.

Interestingly enough there have been recorded marked genetic differences between inbred strains of rodents, not only in respect to their balance of hormones or of vitamins which are natural elements in their biochemical make-up, but in their reaction to influenza or to yellow fever which are caused by agents utterly outside the experience of the ordinary laboratory rodent.

The discovery of this field of inherited differences in hidden potentialities is a fascinating one, for it suggests that by subjecting animals to a great number of foreign stimuli additional genetic units or complexes will be discovered. In forms, such as mammals, which breed slowly, any method of supplementing the tantalizingly infrequent process of mutation is a welcome weapon for research.

The recognition of the importance of knowing the genetic background of the material used in experimental medicine has spread rapidly. It can largely be credited to the repeated unavoidable and insistent demonstration of this fact by rodent material. This is a great contribution to the advance of human biology. It takes a repeated and varied demonstration of the miracles of the genetic Moses to impress permanently the hard heart of the Pharaoh of the medical profession; and it is necessary to influence that worthy group because by its manipulation of man's ignorance it holds in bondage the application of recognized biological principles to human material.

The emphasis on genetics which results from studies on laboratory rodents is also having a very definite effect, by lifting the fog of misunderstanding and erroneous information which has led the medical profession to speak of "hereditary syphilis" when it meant "transmitted." These two processes, "heredity" and "transmission," have remained in narcotized confusion in the medical mind for decades.

II

Other facts made patent by experiments with rodents have had a most salutary effect upon the over-enthusiasm of those organizers of post-Mendelian eugenics who, like the fond parents of a child with some dramatic talent, attempted to make their immature offspring something that it was not. The memory of those days when worthy ladies and gentlemen rushed their half-clad infant genes for all sorts of strange physical peculiarities and mental maladjustments, upon the stage of eugenic literature, is still green to many of us. It is, however, the green of the oyster and not of the laurel wreath.

Only the evidence derived from experiments with rodents has prevented the mathematically subdivided man of Galtonian heredity from being reconstructed as a modernistic mosaic Frankenstein of genes for every conceivable characteristic from nystagmus to wanderlust and from hypospadias to insanity,—which is probably a good place to stop.

The rapidly rising tide of recognized complexities in the genetics of rodents has been effective in showing us that what looked like solid ground was dangerous and shifty mud. First, naturally, were experiments that showed exceptions to clear-cut Mendelism—different types of spotting that did not segregate properly; many genes that influenced a single character, many characters that were influenced by a single gene; normal “overlaps,” the living reminders of a widening gap of uncertainty lying between genotype and phenotype. These things showed the danger of too simple a conception of human biology. They even went so far as to begin to divide geneticists into two very distinct groups—those who tried to bind up the wounds which a cruel world had inflicted on the still toddling infant, “human heredity,” and those who walked by (some I regret to say chuckling eerily) on the other side of the street.

Those who chose the latter course might have gone on in smug self-satisfaction had not the brilliant analytical

methods devised by Wright made them suddenly aware that their own armor was not any too sound. It was not only man who presented difficulties. Laboratory rodents were forcing upon man a picture of the complex relationship between genes and development and between intrinsic and extrinsic factors, that has completely made over his approach to his own biological problems.

The need of direct observation to replace pedigrees reconstructed from socio-biological data gathered by eugenic sleuths became admitted and forms to-day a *sine qua non* of research in human biology. When transferred to a problem which lasts for many generations this principle demands patience and permanency of an investigation over a long period of time. The relative importance of any one individual investigator at any one time becomes less, and that of a well-established program of research, more.

The futility of relying upon small numbers of individuals impresses itself more and more upon the investigator. The difficulties encountered even with the easily recorded, readily measured characters in abundantly prolific laboratory rodents say clearly to the human biologists "Stop, Look and Listen" before crossing the railroad track which divides speculation from accepted proof.

III

But it may be felt that all that laboratory rodents have contributed to the better understanding of human biology is confined to our digging, with hard facts and difficulties, the grave in which the fruits of the premature conceptions of that subject are buried. This is far from being the case.

There are two levels on which the experimental results obtained with laboratory rodents influence most vitally and constructively the course of development of some of the most important principles of biology as applied to human beings.

The first of these levels is that provided by the fact that

the life span of laboratory rodents is of the right length to present an opportunity for continuous study of the successive chemical, morphological and physiological stages which characterize the history of the individual mammal from conception to death. This is a definite and concrete contribution to the solution of problems of human biology.

The second level is less easy of definition. It is that of the effect which the facts derived from a study of rodents have upon the socio-biological philosophy of our generation. Very evidently in spite of its somewhat intangible quality this influence of laboratory rodents may, if constructive, be broad in extent and of great lasting importance.

Let us first return for a short time to the consideration of the more definite and central ring of influence—that of the convenient life cycle—before taking up the wider ripples which lap against more speculative shores.

The existence of a considerable number of different genetic strains of laboratory rodents, notably mice, is the result of a program of intensive inbreeding, sufficiently prolonged to have produced within each strain a high degree of genetic homogeneity.

Within any such inbred strain the transplantation of tissue, either normal or tumorous, is ordinarily as successful as is transplantation of a bit of similar tissue from one part of an individual's body to another. On the other hand, successful transplantation outside of the inbred strain is ordinarily much less frequent and is often entirely impossible. The rate at which individuals of a certain strain eliminate the foreign tissue placed in them varies according to several factors. Chief among these is the age of the individual receiving the implant. The foreign tissue persists for a longer time in very young animals and in very old animals of an inbred strain than it does in young adult animals. Translated into general terms this means that the full expression of the genetic characteristics of the strain, which enables it to recognize the implanted tissue as foreign, is gradually acquired and, as senility comes on, is gradually lost.

Similarly, if *variation* in a given physiological function is studied at different ages of the individual it will prove to be greater when the individual is at the age when the function begins, less as the individual approaches the peak of its physiologic efficiency at the young adult stage and then greater again in old age.

These two lines of evidence contribute very importantly to our understanding of mammalian individuality—a term at once both essential and difficult of definition. We are perhaps too prone to focus our attention upon the relatively clear morphological limits within which an individual mammal is confined. This gives us a false sense of definiteness and of permanency. The truth of the matter is that the characteristic attributes of mammalian individuality are its reactions and physiological potentialities at any given time. These reflect much more accurately the qualities which make the animal typical of a given strain or species than do the variations in morphology which cater to our most subtly deceptive sense—vision.

From a large number of observations on laboratory rodents we can conclude that the nature of mammalian individuality is that of a complex process which has a durational phase and that it is the product of a balanced and relatively constant internal environment gradually acquired, retained for a time and then gradually lost.

IV

The bearing of this conclusion upon the study of human biology is very evident. Chronological age in mixed genetic material at once loses much of its significance as a factor of individual importance unless the degree to which relative elements and characteristics have developed is also taken into account.

This of necessity drives us back to investigation of the phenomena of experimental embryology, experimental morphology and physiology so that ontogenetic correlations between various structures and/or functions can be

detected. By investigation of this kind with known genetic strains of laboratory rodents with short life cycles it may be possible to shed some light upon the now almost impenetrable darkness of man's internal environment, as it stretches from the fertilized ovum through adolescence and adult life to senility and death. And though there may be delay and difficulty involved in such investigation, we can confidently say that without the use of laboratory rodents to give us the main points of importance applicable to the long and involved life cycle of man, we shall not succeed in solving the problem.

The vast importance of the short life cycle of laboratory rodents is nowhere more evident than in studies of the so-called degenerative diseases, which really mean those conditions of unbalance in the internal environment which indicate that centralized control of function has begun to break down.

Among these cancer is perhaps the classical example. At all events, it has held the center of the stage of public interest for some time because of its growing menace as a cause of death. The contribution made by laboratory rodents to our knowledge of the various manifestations of uncontrolled growth (known as cancer) is an impressive one. It includes data based on the rate of incidence of uncontrolled growth of various types of tissue in different inbred strains. These data have once and for all enabled us to state that the causes leading up to a change from normal to cancerous tissue are multiple and very varied in type.

This line of research also definitely links ovarian hormones and perhaps others as contributing factors which influence the incidence of cancer of the breast. Here, by holding genetics constant and varying the degree of function of internal secretions, and then by reversing this process, we have been able to make real progress in our understanding of how both genes and endocrine glands may interact to produce a given end result. It further emphasizes the glaring defects in our knowledge of the

period attendant upon the mammal's change from intra-uterine to post-natal life. There is evidence which suggests that in mammals this may be a period of a far more critical degree of biologic elasticity and adaptability than we have, up to now, appreciated. This line of research also gives us new and convenient indicators of physiological longevity and in fact opens the door to a whole host of different and fascinating avenues of attack on problems basic to our understanding of man as a mammal in relation to his own complicated internal environment.

V

One might continue indefinitely the discussion of the contributions which the laboratory rodents have made and will undoubtedly continue to make in this field. Since, however, time is limited, it may be well to give an example or two of the less tangible but not less important contributions which laboratory rodents have indirectly made towards the development of a sane attitude in human biology.

The first of these that I shall mention has a certain lighter side. We are all aware of the emotional bubbling and irrational babbling of that strange fellowship of the anti-vivisectionists which pours in a stream over the paralyzed or bewildered brains of legislators at every opportunity and which in such sun-struck states as California has recently become a menace to scientific research. What we do not perhaps realize, however, is that within the ranks of that sturdy body it has been difficult to keep at fever heat a level of sympathy for the rodent similar to that which the dog or cat engenders. Were it not for the appearance of rabbits upon Easter cards and its resultant heart throb, the rodents would be a completely constructive element. The age-old enmity of woman and the Muridae may yet save the day. Seriously, however, the division of forces and the resulting restriction of objective among the anti-vivisectionist, caused by the cold and impersonal eye of rat, mouse, guinea pig or rabbit, is a real

contribution. It may make the rank and file of citizens understand more clearly the abnormal nature of the unbalanced and starved emotions that lie at the base of organized attempts to destroy scientific research with mammals. Since without that research human biology is doomed, the issue at stake is a truly great one.

Another intensely interesting field in which research work with laboratory rodents has exerted an important influence on human biology is that of experimental modification of the germ-plasm. When in 1923 the writer and Bagg published evidence of a genetic modification following the treatment of mouse ovaries with x-rays that agent was being extensively used to correct irregularities in the human menstrual cycle. Little attention was being paid to the subsequent reproductive history of a woman so treated, although certain medical investigators believed that they had evidence of an increased proportion of monsters among children produced following treatment. There is, however, clear evidence that to-day—fifteen years later—a great deal more caution is being exercised. This is because of the fact that although the radiologist applying the rays may not be concerned directly with abnormalities that may crop out in a second or third generation it is recognized that *some one* has to deal with them eventually, once the germ cell change has occurred.

Similarly, the incidence of damaged progeny resulting from injured germ cells which can still fertilize or be fertilized, has been demonstrated in rodents. This fact has or should have a permanent effect upon those who advocate research in contraception by any technique which kills germ cells—unless—and it is an important condition—the treatment kills *all* germ cells and does not include the possibility that some may be injured and still function.

Here then, by making laymen and the medical profession assume responsibility, not only for the generation produced under their immediate supervision, but for those which in the future may bring out hidden abnormalities resulting from ancestral injuries, the laboratory rodents

have performed a very great and impressive service. They have awakened a new sense of the importance of building for the distant future as well as for the present.

There is, moreover, another way in which the laboratory rodents have done a great and lasting service to those of mankind who are not to-day blinded by emotion disguised as pseudo-science. They have made racial "superiority" and "inferiority" antiquated terms in human biology. They have done this in various ways but chiefly by giving us living examples of the unsoundness of many of our former ideas and of the terms which we very glibly used to describe them.

By providing overwhelming evidence of the complex genetic situation in "strains" of laboratory rodents, the implied value of such terms as "race," "strain" and "family" among the vastly more complicated human "genetic" groups has disappeared. When it was obviously none too easy to find any satisfactory criteria of qualitative differences between *species* of laboratory rodents it was impossible to become as aroused as formerly over supposed "racial" or "national" superiority-differences between human beings of the same species.

The philosophy which thus arose from the evidence obtained in the rodent laboratory is one which very definitely relegates the troublesome and stupid distinctions which agitate the world to-day to the realm of propaganda without scientific basis.

We know that we can, under different environmental conditions in the laboratory, develop by selection strains which differ genetically from one another so that very dissimilar end results are obtained. The superiority and inferiority of these end products is, however, a matter which depends entirely upon the circumstances in which they are placed. There is no doubt that to one type the others may be pleasant or unpleasant, welcome or unwelcome. That these reactions are determined by a fixed and ingrained biological superiority or that, between a given characteristic and its basic value, there exists an anthropological

and age-old relationship is, however, entirely unsupported by scientific evidence.

And if in answer to this those who still insist that we must have distinctions appeal to man's psychological and social inheritance as of prime importance, the ample and insistent evidence derived from the humble laboratory rodents leads us back, even though we be blinded, to the conclusion that neglect of biological foundations can and will upset the best-laid plans of sociological reformers or eloquent demagogues.

In a world in turmoil because of unsatisfied greed it is not a bad idea to seek refuge in research concerning man and more especially his inner biological nature. We shall find that his worst enemies still lie there. He is still bound by the very nature of his biological organization in a tangled net of little-understood phenomena. I suspect that research with laboratory rodents will be in the future, as it has been in the past, the chief means of breaking one by one the strands of that net. I suspect that the gnawing of the teeth of mice, rats, guinea pigs and rabbits upon the bonds of man's ignorance will be heard long after dictators stop their bellowings, long after armed strength is paraded for the last time across the great squares of man's stone-blind stupidity and long after we in America stop worrying about the idea of democracy and make it an actuality.

THE USE OF THE MONKEY AND APE IN THE
STUDIES OF HUMAN BIOLOGY, WITH
SPECIAL REFERENCE TO PRI-
MATE AFFINITIES¹

DR. CARL G. HARTMAN

DEPARTMENT OF EMBRYOLOGY, CARNEGIE INSTITUTION OF WASHINGTON,
BALTIMORE, MARYLAND

THE chief subject for the study of man will always be man himself. For the discovery of fundamental principles applicable also to man, however, it may be and has been in the past *Ascaris* or *Drosophila* or the white rat. Where lower animals are suited to answer our questions and help solve our problems it is extravagant, often undesirable for other reasons, to use the monkey. Because of the limitations of experimentation on the human being, however, in order to bridge the gap from the lower forms to man, primate animals must be the subject of choice. For three lines of investigation, apes and monkeys would seem to be indispensable: the study of certain diseases; the origin and affinities of man; problems of reproduction, notably menstruation. One might add problems of neurology; but I prefer to discuss these briefly under the second head. Of the first I know little; in the second field some of my friends have over a period of years attempted to orient me; in the third I hope to make a small contribution to the subject through first-hand information and to show how some recently acquired knowledge of reproductive processes in apes and monkeys substantiate the general conclusions that have previously been drawn on morphological evidence.

We may dismiss the subject of special susceptibility of monkeys to certain human diseases with the remark that this is just another evidence of the close affinity of monkeys to man.

¹ Read at a Symposium of the American Society of Naturalists in joint session with the American Society of Zoologists, the Botanical Society of America and Section H, The American Association for the Advancement of Science, Richmond, Virginia, December 30, 1938.

In attempting to gain a bird's-eye view of the chief lines of evidence bearing upon man's place in the order of primates we become aware first and foremost of an array of studies on the configuration of (a) the teeth; (b) the skeleton. This preponderance of data on the hard parts of organisms is due partly to the fact that skins and skeletons alone are suitable for convenient transportation from the field; the perishable soft parts usually have of necessity to be left behind. Furthermore, the soft parts do not lend themselves as readily to metric analysis and among higher primates differ qualitatively even less than the hard parts. Since dental and skeletal measurements have the advantage that great accuracy is attainable, the data may be plotted on curves for comparisons from species to species.

A perusal of the literature discloses the fact that several generalizations may be made without arousing too much opposition from one quarter or another (*cf.* Wool-lard, 1938).

First, there exists to-day no "contemporary ancestor" of man—no primate in the process of becoming human. In other words, each species occupies an end-twig of the family tree and each group has differentiated in its own way since leaving the ancestral stem. Concerning the comparatively few fossil primates thus far unearthed, there is no agreement as yet among paleontologists as to whether these constitute true "missing links" in the direct line of descent or mere side-branches on a par with the 600 living species of primates.

A second conclusion seems imperative, that a valid seriation of primate groups on the basis of degree of resemblance to man or to chimpanzee or to the rhesus monkey must consider a great many characters. As Schultz has repeatedly shown, an arrangement in respect to the degree of development of one character may or may not hold for another character. If the characters are weighted for degree of importance and the data treated statistically one finds in general that the anthropoids re-

seemble man much more than do lower monkeys; that catarrhines (Old World monkeys) form a group nearer to man than the platyrrhines (New World monkeys); that chimpanzee and gorilla form a closely related group somewhat distinct from the orang-utan and still farther removed from the Hylobatidæ (gibbon, siamang). Taking the most studied chimpanzee as an example of the anthropoids and the rhesus monkey as the most studied catarrhine it is true that in many characters the chimpanzee is more or less intermediate between monkey and man. We shall a little later add several new items that fall in line with this thesis.

While man has differentiated in his own way in numerous characters we appropriately call "human," he also possesses characters which may be designated as primitive, inasmuch as, according to Straus, they resemble those of the platyrrhines rather than the apes or higher monkeys. It would seem, therefore, that he deviated from the ancestral stem in early geological time, since he carries those primitive characters. The family tree of Weinert (Fig. 1) must be wrong, that of Schultz and that of Gregory more nearly in line with the facts.

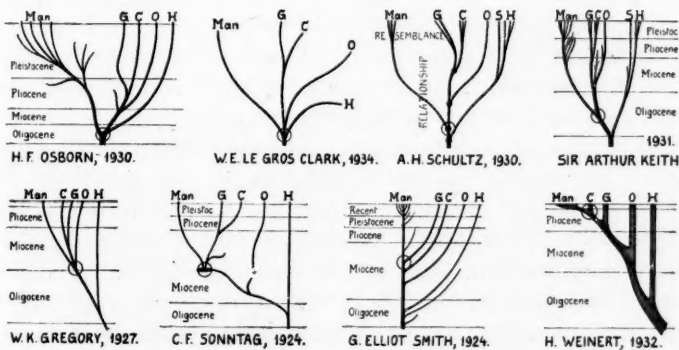


FIG. 1. The family tree of the higher primates according to different authorities. G, gorilla; C, chimpanzee; O, orang-utan; S, siamang; H, gibbon or Hylobatidæ in general. From Schultz, 1936.

A final conclusion is impressed upon the non-specialist reading in this field of anthropological study, namely, that

the science of primatology has but begun. Not only must we know something of many more species, but we must know a great deal more about the few thus far investigated on inadequate material.

If this be true of the more accessible hard parts of the organism what hiatuses do we not see in respect to our knowledge of the growth and variations of the soft parts? These have not as yet entered much into the calculations of either the taxonomist or the anthropologist, since data from one or two specimens of each species have very limited significance and since adequate series of properly preserved specimens are rarely obtainable and few investigators have the infinite patience needed for dissecting them. The growth of the skeleton depends, indeed, upon the action of soft parts: anterior pituitary, parathyroid, gonads, all under the final aegis, of course, of the genetic constitution. As an example of a study of soft parts checking and corroborating that of skeletal parts and teeth, the rabbits and hares might be cited, which, on the basis of skeleton and teeth, Gidley removed from the *Rodentia* and created for them a new Order, the *Lagomorpha*. One thinks at once of certain other characters that argue strongly in favor of Gidley's contention: (1) the albumen-covered ovum, (2) the interstitial cell-laden ovary, and (3) the comparatively simple method of early development and implantation of the rabbit as compared with all the known Rodentia (Hartman, 1925).

The many hiatuses in our knowledge of primate morphology, until corrected, will continue to stimulate absurd interpretations of human structures. It is too easy to say: "Not found in any subhuman primate"—which may be correct but is misleading, for the point at issue may not have been investigated. To cite an example: In our youth we were taught that because man possesses an opposable thumb (barring the lowly opossum, which apparently did not count), he is also the only being provided with the appropriate muscle (*M. opponens pollicis*). The hard fact stands, however, that all species of apes, monkeys and even lemurs thus far studied possess this muscle, though

its size may be variable and the proportion of individuals within the species in which it is absent varies from species to species. Moreover, the opposability of the thumb is a primate character and, as Schultz has shown, the species as a matter of fact differ only in degree of opposability.

Next to the skeleton it is the primate musculature which has received the greatest amount of attention, first by the Swiss anatomist, G. Ruge, whose mantle fell upon the late E. Huber, who brought to the Johns Hopkins Ruge's spirit and techniques. Huber's work on the comparative anatomy of the facial musculature and its innervation; likewise that of Howell and Straus on the general musculature of the rhesus monkey, accompanied by comparative notes, are outstanding in their extent and thoroughness. For seriation of the primates these studies have, however, led to discordant results. Thus the human hand is primitive as compared with that of the chimpanzee, and more like that of lower primates. In consonance with this conclusion we see that an infant when it walks on all fours lays the hands down flat like a rhesus monkey, not flexed, with knuckles on the ground, like chimpanzee or gorilla (Hrdlička). On the basis of his studies on the viscera also Straus finds that man has a greater similarity to the more primitive Old World monkeys than to the anthropoids.

Compared with primate anatomy our ignorance of primate physiology is even deeper and wider, as has been shown by Zuckerman in his interesting book, "Functional Affinities of Man, Monkeys and Apes." These gaps should be filled, for it is true that "every structure and property of the animal or plant, whether they be organs or cytological structures, physiological activity, habits or ecological relationships," constitute characters of potential value for taxonomy or phylogeny.

Thus far physiological data of phylogenetic value have come from three main lines of investigation: (1) Blood groupings and agglutination phenomena; (2) physiology of the nervous system; (3) physiology of reproduction.

The precipitin reaction already in the hands of Nuttall

gave quantitative indications of the relationship of the primates. In these experiments the anthropoids approached nearest man, the platyrrhines appeared furthest removed. For more accurate because more delicate tests we turn to the experiments of Landsteiner and Miller (1925), Mollison and others, who worked with blood-group specific isoagglutinins. Since each blood-group has its specific agglutinin, a rabbit may be immunized to a particular agglutinin and its serum then tested against the corresponding class of blood in the species studied. Landsteiner and Miller and those who repeated and extended their observations have concluded in general that the blood of the anthropoid apes and that of man are practically identical by these tests and that the Hylobatidae, the catarrhines and the platyrrhines form sharply separated groups, each, however, closely related *inter se*. Other immunological phenomena, on the other hand, give results inconsistent with the seriation thus outlined. While it is evident that too few tests have been made on too few species, largely because of the lack of available specimens, on the whole the blood tests show the great apes intermediate between man and monkey but much closer to man.

Neurological investigations, the most extensive and varied of which we owe Fulton, corroborate this conclusion: In brain size as well as cyto-architecture the anthropoids are far removed from all monkeys, approaching man, though never reaching him even in absolute brain weight. Of particular interest is the Babinski reflex thus far observed only in man and chimpanzee.

The rapid advance in the field of reproductive physiology in the last several decades has been reflected in a considerable growth of our knowledge of reproductive processes in the primates. The availability and hardiness of the rhesus monkey has made this species the chief laboratory primate. The groundwork on the chimpanzee has been accomplished by the Yale Laboratory of Primate Biology, so that this rare, huge man-ape has taken its place beside the white rat, guinea pig and rhesus monkey. In

the near future we may look to the Columbia University project in Puerto Rico for equivalent knowledge concerning the gibbon. The platyrrhines of the Old World still remain almost totally *terra incognita*.

For the experimental study of menstruation the monkey is absolutely indispensable, since only the higher primates exhibit this phenomenon either spontaneously or in response to hormonal treatment. If one injects the female sex hormone into castrated rabbit doe and castrated female monkey, the uterus in either case will grow for a time during the administration of the hormone and in either case, after cessation of injections, the uterus will rapidly regress. The monkey uterus will bleed (menstruate) in characteristic fashion, the rabbit uterus will not. The two species are as distinct with reference to this character as to any other character, for example, their vision, the monkey having stereoscopic vision with overlapping fields, while the rabbit sees an object out of one eye at a time.

Anatomically, the difference in the two uteri lies in the peculiar spiral arteries of the monkey endometrium. In the physiology of these arteries, universal among primates, lies the mystery of the menstrual flow.

So far as known, the uteri of man, apes and catarrhine monkeys have all essentials in common. Only the little-known platyrrhines may be expected to yield some exceptional traits. We already know that their uterine glands are tremendously developed and active (Table 1).

Because of the similarity of primate uteri and the associated menstrual process, experimental findings in the monkey may be directly applied to women, as clinicians are beginning to realize. The rhesus monkey, therefore, occupies a key position for the experimental probing into the cause of menstruation. It follows from these remarks, however, that the study of menstruation will yield little of phylogenetic value within the group, at least until we know more about the platyrrhines. In point of length of the cycle Yerkes and Elder have found the chimpanzee cycle to average at least a week longer than the average

TABLE 1
PLACENTAL EVIDENCE OF PRIMATE RELATIONSHIPS

Character	Man	Anthropoids (Chimpanzee)	Catarrhines (Macaques)	Platyrrhines (Howler, Spider)	Tarsius
Implantation:	Interstitial	Interstitial	Superficial	Very superficial	Superficial
Decidua capsularis	Yes	Yes	No	No	No
Villi	On all sides	On all sides	Partly lacking	Partly lacking	Partly lacking
Villi formation	Precocious	Precocious	Precocious	Delayed	Precocious
Lacunae in trophoblast	Simple	Simple	Simple	Labyrinthine	Prob. Simple
Decidual reaction	Marked	Marked	Moderate	Moderate	Prob. Moderate
Epithelial plaques	Absent	Absent	Thick, localized evanescent	Thin, extensive long persisting	Thick, localized
Definitive placenta	Human or "villous" type	Human or "villous" type	Human or "villous" type	Trabeculated, Labyrinthine	Trabeculated, Labyrinthine
Uterine glands	Single	Single	Mostly double	Double or single	Considerably developed
	Moderately developed	Moderately developed	Moderately developed	Markedly dev. and active	

of a lunar ("menstrual") month, obtaining in women and the catarrhines (Fig. 2). In consonance with the long

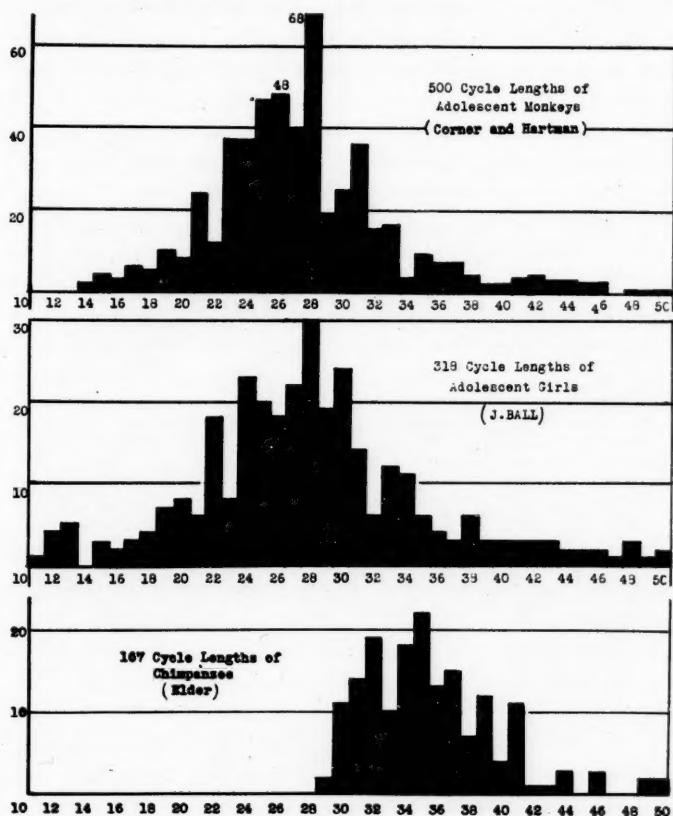


FIG. 2. Graphs of cycle lengths of young monkeys, girls and mostly adult chimpanzees. The graphs for women and adult monkeys would show a little less spread but the same average.

cycle, ovulation in the chimpanzee is also delayed by a week. Hamlett has adduced evidence that the platyrrhines experience two complete cycles in a month. If this is corroborated we have two groups that have differentiated in their own way with reference to the menstrual cycle.

The definitive placenta offers little ground for seriation of the primate groups, except to separate the platyrrhines from the higher members. For, while the primate placenta is sharply differentiated from that of all other mammals, the human, anthropoid and catarrhine placentae present a common type *inter se*. It is in the main only in the early stages that it is possible to differentiate them.

The early development of the placenta is adequately known, from its beginnings, for only one primate species, the rhesus monkey. Based upon a complete series of accurately timed specimens furnished by the Carnegie colony, this chapter in primate biology has been written within the year (Wislocki and Streeter, 1938). The specimens are perfectly preserved and impeccably prepared by my colleague, Dr. Heuser. Human material is next in order of completeness, though the earliest embedding of the ovum, covering a period of two days, is absolutely blank and the condition of specimens beyond the eleventh day (age of the youngest human ovum, the "Miller") often leaves much to be desired. Aside from these two series the 600 species of primates to this good day are represented by only a score of fairly young embryos and implantation sites (gibbon, catarrhines, platyrrhines, Tarsius and the lemurs). By a fortunate set of circumstances we are able to-day to present a 10½-day chimpanzee ovum, furnished by the laboratory of our honorable president, Dr. R. M. Yerkes. Further reference to this beautiful specimen will be made presently.

The features of placentation in primates which seem to me most significant from a comparative standpoint have been condensed in the accompanying table. In the preparation of this I have drawn upon the important monograph of Hill (Croonian Lecture, 1932), that of Wislocki and Streeter (1938) on the rhesus monkey as well as the extensive materials of the Carnegie Laboratory of Embryology. We may restate the contents of the table as follows:

While all primates (excepting the lemurs and Prosimiae) exhibit the burrowing type of placentation, only

in anthropoids (including the gibbon) and man does the vesicle burrow completely beneath the uterine epithelium. This has been known for the orang-utan and the gibbon (Selenka, 1899) because their implantation sites exhibit a decidua capsularis, the more superficial portion of the placenta where villi are imperfectly formed. No early stages were, however, known for any anthropoid until the discovery of the 10½-day chimpanzee which we are able to present to-day (Fig. 3, B). This specimen is about a half-day younger than the youngest captive human (Fig. 3, A).

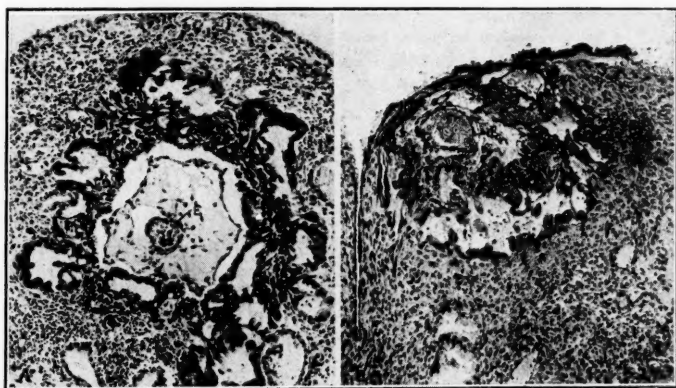


FIG. 3. (A) The "Miller" ovum, the youngest normal human embryo thus far known. From Streeter, 1926. (B) Chimpanzee ovum, "Yerkes A," the youngest known anthropoid ovum. From Elder, Hartman and Heuser, 1938.

The illustrations show the similarity between the two, which is as complete as imaginable, considering that the chimpanzee is a little younger and smaller and much better prepared than the Miller ovum, which was accidentally found amidst the debris of curettings. The cardinal point is that at 10½ days the anthropoid vesicle is already surrounded on all sides by maternal tissue.

Already in the youngest anthropoid and the youngest human ovum the trophoblastic shell has developed lacunae, although in these there is as yet no extravasated maternal blood. These lacunae enlarge into irregular spaces which

remain fairly simple in all Simiae except the platyrrhines in which the structure becomes very complex by virtue of a profuse growth of trophoblastic trabeculae. Since the condition is also simple in *Tarsius* we may consider the complex nature of the platyrrhine trophoblast as a unique specialization.

A decidual reaction, that is, enlargement and succulence of stromal connective tissue cells, is most pronounced in man and the anthropoid apes. The reaction is much less marked in the rhesus preparations in our possession. But the most striking character, sharply differentiating the lower monkeys from the man-anthropoid group, is the reaction of the uterine epithelium to the "sting" of the ovum. In the vicinity of the points where the 9-day vesicle touches the epithelium this proliferates and thickens, forming thickened epithelial cushions or weals, one on the ventral surface, usually the primary one, and one on the dorsal surface (Fig. 4). These epithelial plaques are con-

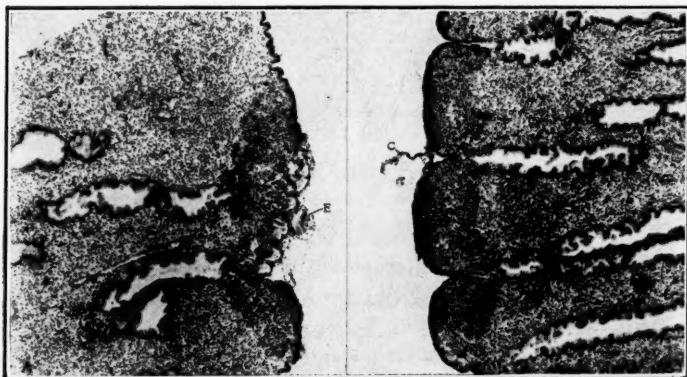


FIG. 4. Sections through endometrium of rhesus monkey C530, showing 12-day embryo (E) and the primary (left) and secondary placental plaques. C, chorion torn loose. From Wislocki and Streeter, 1938.

sumed by the invading trophoblast and form the pabulum of the ovum for about 10 days. No plaques are produced in the human or anthropoid uterus, but in all monkeys and in *Tarsius*. The placental plaque in the catarrhines and

in *Tarsius* is thick and localized, in the platyrrhines, thin, extensive and more persistent. While this again breaks the linear series—*Tarsius*→*Platyrrhines*→*Catarrhines*→*Anthropoids*→*Man*—the character does once more sharply set man and the anthropoids off from the remaining primates.

The characteristics of the very young embryo proper can not yet be utilized for purposes of primate phylogeny because of the meager data at hand. Incidentally it might be mentioned that the four free vesicles included in the collection of rhesus ova conform strictly to the mammalian type. We can confidently conclude that the bilaminar vesicle of man and the anthropoids will eventually be found to conform likewise.

On later prenatal and postnatal growth of the primate data are in hand for man, the rhesus monkey and to some extent for the chimpanzee. The first adequate human series for the study of prenatal growth we owe to Streeter and Schultz. Seven hundred fetuses of the Carnegie collection, mostly from pregnancies with fairly good menstrual records, formed the basis for these studies. Moreover, since each investigator personally measured all the specimens the variable personal equation inherent in compilations from numerous sources was eliminated.

To date, the story of the growth of but one primate animal, the rhesus monkey, has been written. At the Carnegie Laboratory we were able to assemble a goodly number of fetuses and young of this species, concerning all of which the conception age was accurately known, mostly to a day. We were fortunate in having available an interested anthropologist, A. H. Schultz, who measured the specimens and interpreted the observations and measurements in the light of human development (Schultz, 1937). In the accompanying chart (Fig. 5) the curves of intra-uterine growth of man and rhesus monkey are shown. It is seen that the monkey fetus grows a little faster than the human fetus until the twentieth week of gestation, when it is overtaken by the latter. From the data furnished by

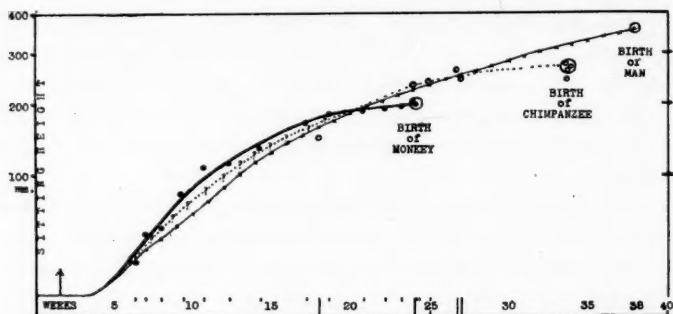


FIG. 5. Growth curves for man (after Streeter, 1920), rhesus monkey (after Schultz, 1937) and chimpanzee (data contributed by A. H. Schultz and Yale Laboratory of Primate Biology). The greater part of the growth curve of the chimpanzee is conjectural, being based on the few cases plotted in open circles. Arrow indicates age of youngest human and youngest anthropoid embryos shown in Fig. 3.

five late fetuses and several new-born babies of the chimpanzee (two cases of which we owe to Schultz, the remainder to the Yale Laboratory of Primate Biology) it seems highly probable that the prenatal growth curve of this species will be found to fall between that of monkey and man and that its growth curve will cross the other two at the 20-week point. We are fairly safe in concluding that at 20 weeks' development the fetuses of monkey, chimpanzee and man are of approximately equal size. We have noted above that the placentae of the three species are so much alike that microscopically they are not distinguishable one from another; hence it is fair to say that a given nutritive tissue, the placenta, is capable in a given time of producing a uniform bulk of baby.

The rhesus monkey is born soon after reaching this interesting point of development. The human baby is larger at birth because it remains longer *in utero*. The chimpanzee is intermediate in this respect. It is also intermediate as to degree of maturity at birth between the very helpless human baby and the monkey baby capable of clinging safely to the mother's body five minutes after parturition.

The chart (Fig. 5) likewise shows the period of gesta-

tion of the chimpanzee (235 days) to be intermediate between the monkey (165 days) and man (267 days). So far as we know the catarrhines in general conform closely to the figures first worked out at the Carnegie colony on the rhesus monkey, namely, 6 lunar months against 10 for man.

To the phylogenetic series—monkey→chimpanzee→man—we are able to add one more functional character. Since Aschheim and Zondek 10 years ago discovered a gonadotropic principle, prolan, in the urine of pregnant women, a search has been made for this principle in the urine of pregnant animals. The results were negative in all but the primates, although in some cases the blood of lower mammals, *e.g.*, the horse, was found to contain enormous quantities of a similar substance. In women it was found that early in pregnancy, around the sixtieth day, prolan is present in the urine in huge quantities, dropping off rapidly to a low titre maintained throughout the remainder of gestation. At the Yale Laboratory of Primate Biology,

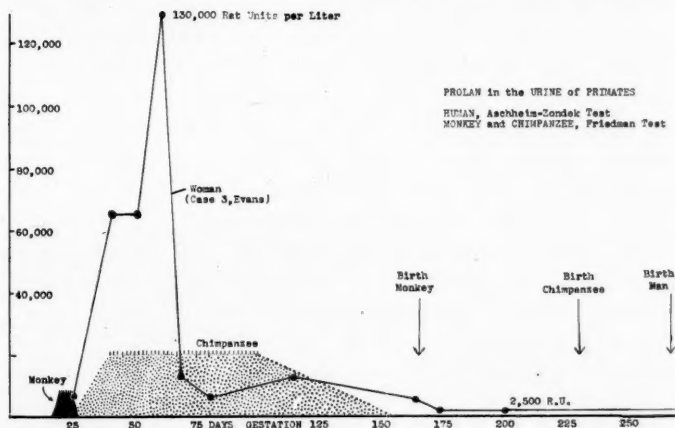


FIG. 6. Chart showing days of gestation in which prolan (gonadotropic hormone) is present in the urine of rhesus monkey, chimpanzee and woman. The curve for woman was determined on rats and is quantitative; those for monkey and chimpanzee by the rabbit test and are not quantitative. Monkey data from Hamlett, 1936; chimpanzee data (from Elder, unpublished) of the Yale Laboratory of Primate Biology.

Elder was able to recover prolactin from the pregnant chimpanzee as early as the 25th to the 35th day and found it to disappear completely between the 100th and the 160th day. Finally, Hamlett, examining pregnant rhesus monkeys of the Carnegie Colony, discovered that in this species the prolactin output was most evanescent, lasting only from the 19th to the 25th day after fertilization. These facts are recorded in the accompanying chart which graphically represents again the phylogenetic series—monkey→chimpanzee→man (Fig. 6).

Nothing has been said as yet concerning behavioral characteristics and relative intelligence. Fortunately we have Dr. Yerkes to discuss this subject.

Weighing all the facts it is safe to conclude that the primates are separable into definite groups distinctive with reference to many characters: anatomical, embryological, physiological, chemical, hormonal. Seriation of groups in respect to degree of resemblance to man varies from one character to another, but on the whole the series runs roughly: (1) man, (2) chimpanzee and gorilla with orang-utan trailing; (3) gibbon and siamang; (4) the catarrhines; (5) the platyrrhines; (6) *Tarsius*. Certainly the great bulk of the data, to which we have been able to add several new items, points to close affinity of the apes to man as compared with the monkey.

The studies here sketchily reviewed in this lecture point, however, to one incontrovertible conclusion, namely, the fragmentariness and meagerness of our knowledge of primates. The attention given primates is but a tiny proportion of that accorded the laboratory and domestic mammals. More projects like the Yale Anthropoid Colony and the Columbia Gibbon Colony should be initiated, especially one for the study of the American monkeys. We need more men like Schultz to exploit the museums, like Zuckerman to make intelligent use of primate collections in zoological gardens, or like Carpenter to go to the animals in their native haunts and live with them long enough really to learn something about them. I mean this

address to be a plea for a more adequate prosecution of primate studies, and I have attempted to show that in this field we have only scratched the surface.

Fully to understand man we must learn all about man's nearest relations (the primates), so that we can finally show what morphological, physiological and psychological features are really peculiar to man and what others man shares with the apes. We must continue to gather facts diligently and carefully. Once the facts have been ascertained, theory, the most useful guide to fact-gathering, will itself evolve and guide us to the truth.

REFERENCES

- Carpenter, C. R.
1934. *Comp. Psychol. Monographs*, Vol. 10, No. 2.
- Elder, J. H., and R. M. Yerkes
1936. *Anat. Rec.*, 67: 119-143.
- Gidley, J. W.
1912. *Science*, n.s., 36: 285-286.
- Gregory, W. K.
1934. "Man's Place among the Anthropoids." Oxford.
- Hamlett, W. G. D.
1937. *Am. Jour. Physiol.*, 118: 664-666.
- Hartman, Carl G.
1925. *Jour. Mam.*, 6: 114-121.
- Hill, J. P.
1932. *Phil. Trans. Roy. Soc. London*, 221B: 25-178.
- Howell, A. Brazier, and W. L. Straus, Jr.
1933. Chap. VII, in "The Anatomy of the Rhesus Monkey," by Carl G. Hartman and W. L. Straus, Jr. Williams and Wilkins Company. Baltimore.
- Landsteiner, K., and C. P. Miller
1925. *Jour. Exp. Med.*, 42: 863-872.
- Schultz, Adolph H.
1936. *Quart. Rev. Biol.*, 11: 259-283.
1937. *Contrib. to Embryol.*, 26: 71-97.
- Streeter, George L.
1920. *Contrib. to Embryol.*, 55: 143-170.
1926. *Contrib. to Embryol.*, 18: 31-48.
- Wislocki, Geo. B., and Geo. L. Streeter
1938. *Contrib. to Embryol.*, 27: 1-66.
- Woollard, H. H.
1938. *Science Progress*, pp. 17-28, July.

THE SEX RATIO IN WILD BIRDS

DR. ERNST MAYR

THE AMERICAN MUSEUM OF NATURAL HISTORY, NEW YORK

UNEQUAL sex ratios in vertebrates have been generally ignored during the last two decades, although they are of the greatest theoretical importance. Only such cases as could be explained on a hormonal basis have been discussed in greater detail. Professor Crew points out in a recent paper (1937) what was generally known but never sufficiently emphasized, that in vertebrates there is an amazing number of exceptions to an expected sex ratio of 50 per cent. males and 50 per cent. females. He concluded that the classical theory of inheritance of sex will have to be modified in several respects in order to comply with the known facts. Unfortunately Crew did not utilize all the available evidence, with the result that his conclusions, though basically correct, are too specialized, as I shall show below. I shall restrict my remarks almost exclusively to birds, since this order of vertebrates was particularly neglected by Crew, who states: "In the case of birds there is much that is anecdotal and a certain amount of information that has been derived from experimentation." This statement implies that Crew considers all the observations of the field naturalists as "anecdotal" and therefore as unreliable. It is easily understandable how Crew could have arrived at such an opinion, since there is no recent survey of the field available. On the other hand, there actually exists an enormous amount of highly valuable evidence which is quite inaccessible to the laboratory biologist because it is scattered through hundreds of volumes of ornithological journals. I have attempted to summarize this vast literature with particular emphasis on such evidence as indicates the occurrence of unusual sex ratios in birds.

PRIMARY AND SECONDARY SEX RATIO

It is convenient for practical purposes to classify observed sex ratios in three groups. The *primary sex ratio*

relates to the proportion of the sexes at the time of fertilization, the *secondary sex ratio* at the time of birth and the *tertiary sex ratio* during adult life.

The three sex ratios will remain identical, if the death-rate of males and females during prenatal and postnatal life runs exactly parallel. It has, however, been found in most animals that the death-rates of males and females differ at every period of life. This difference may be caused by genetic factors (sex-linked lethals) or it may be due to physiological factors (different rates of metabolism) or to environmental factors (such as differences in vulnerability toward dangers). This means that an exact knowledge of all three sex ratios is required before one can analyze the underlying causes for the deviation from the normal ratio.

The primary sex ratio of wild birds is easily obtained because it equals the secondary sex ratio in all those broods where the complete clutch of eggs hatches. It is, therefore, rather surprising that so little evidence on primary sex ratios in birds has yet been published. It is much more difficult to arrive at definite figures for the primary sex ratio in the domestic hen which lays continuously, particularly where heavy mortality in the eggs is involved. Consequently no data on this have yet been published. The actual figures on the primary sex ratio in the genera *Cassidix* (see p. 172) and *Larus* (see p. 158) will be quoted below.

The secondary sex ratio is reasonably well known for a number of domesticated species (see also Crew, *op. cit.*, p. 546). The greatest amount of information concerns the domestic fowl. All the evidence is summarized by Byerley and Jull (1935) who found among 96,008 chicks, alive at hatching, 49.17 ± 0.11 per cent. males, a figure which deviates sufficiently from the ideal 50:50 ratio to be of statistical significance. In the pigeon, on the other hand, Cole and Kirkpatrick (1915) found a secondary sex ratio of 105♂:100♀. Crew quotes some additional figures, but in none of the cases (except in hybrids) did the

secondary sex ratio vary more than 5 or 10 per cent. from the ideal 50:50 ratio.

Very little is known about secondary sex ratios in wild birds. There are, of course, scattered through the ornithological journals quite a number of statements concerning the number of males and females among the young in a single nest, but the number of nests that were investigated was too small to be of any statistical significance. The few available data indicate a rather high proportion of males among Passerine birds. All the evidence has been ably summarized by F. Groebbels (1937).

How little such scattered data signify is particularly well illustrated by MacDowell and Lord's (1925) work on the house mouse, which showed an almost ideal primary sex ratio (416♂:415♀) in 106 litters. In single litters, however, the sex ratio was often unequal, for example: 3♂:6♀, 1♂:7♀, 7♂:3♀, 7♂:1♀, etc. Something very similar was shown by F. Goethe (1937) in his study on the primary and secondary sex ratios in the herring gull (*Larus argentatus* (L.)). In 14 complete clutches with 3 eggs he found the following sex ratios: 0♂, 3♀ (4 times), 1♂, 2♀ (3 times), 2♂, 1♀ (3 times), 3♂, 0♀ (4 times). In 11 clutches with 2 eggs he found once 0♂, 2♀, twice 2♂, 0♀, and 8 times 1♂, 1♀. The total of 64 young birds yielded 33♂ and 31♀, a remarkably close figure in view of the small number of clutches that were examined. This strong random variation invalidates the significance of most of the material quoted by the older ornithologists (Liebe, 1894; Heinroth, 1912; Lucanus, 1917).

Additional material on the secondary sex ratio in the genera *Accipiter* (p. 168), *Psaltiriparus* (p. 166) and *Casidix* (p. 172) will be discussed in later paragraphs.

THE TERTIARY SEX RATIO

Cytologists and geneticists are chiefly interested in the primary and secondary sex ratio, as illustrating certain cytological and genetic phenomena. The student of animal populations, the ecologist, the student of reproductive

behavior and the naturalist are, however, principally interested in the tertiary sex ratio, that is, the proportion of the sexes in adult populations during the period of reproduction. The great importance of the adult sex ratio has long been recognized by the student of human populations, but it has not received as much attention from the animal biologist as it deserves. The principal reason for this neglect has been the difficulty of determining the true sex ratio in adult populations. Furthermore, an "adult" population is never homogeneous, but rather composed of a whole set of age classes. There is also rarely a random distribution of the sexes because a number of environmental factors tend to segregate them. However, it can be shown that all these objections do not obliterate the value of the tertiary sex ratio, provided that a reliable technique was employed in the determination of this ratio.

METHODS AND SOURCES OF ERROR

The methods used for the determination of the tertiary sex ratio are largely determining the value of such figures. They can be used by the general biologist only if all possible errors are eliminated. A truly representative adult sex ratio can only be expected if the two sexes never segregate during seasonal movements nor differ in their habits to such an extent as to make counts unreliable. Such ideal conditions rarely exist in birds. How much these factors may influence sex ratios that are actually nearly balanced shall be shown in a few examples.

The influence of migration: Every ornithologist knows that the migration period of the male bird is in most species different from that of the female. The males usually return in the spring several days to weeks earlier than the females and may leave later in the fall. There is usually a preponderance of males in the winter populations of those species in which only part of the population is migratory, such as in the song sparrow (*Melospiza melodia*). M. M. Nice (1937) found during the breeding season an almost balanced sex ratio of this species in the

Interpont area near Columbus, Ohio. But owing to the departure of a greater proportion of the females, there were the following percentages of males caught in her traps (among more than 1,000 captures) during the winter months: September 52 per cent., October and November 70 per cent., December to February 74 per cent., March 67 per cent., and April-July about normal again. This stronger migratory urge of the females also expresses itself in the figures quoted by Drost (1935) for birds caught on the island of Helgoland during migration. In the eleven years 1924-1934, 1,092 males of the blackbird (*Turdus merula*) were caught during the fall migration against 1,631 females (59.9 per cent. ♀). During the spring migration the ratio was still more unequal, 1,846 males against 3,636 females (66.3 per cent. ♀). Still there is no evidence of a strongly uneven sex ratio during the breeding season. One of the best illustrations of the influence of migration time and situation of the winter quarters on the sex ratio is given in the figures published by Heydweiller (1936) on the composition of the flocks of tree sparrows (*Spizella arborea*) observed near Ithaca, New York. The proportion of sexes in these flocks was as follows:

October-December 15	♂ 50-60%	♀ 40-50 %
January 1-March 15	♂ 85	♀ 15
March 20-March 25	♂ 70	♀ 30
March 28-April 16	♂ 40	♀ 60
April 24-April 26	♂ 15	♀ 85
May-September	♂ absent	♀ absent

A wealth of similar data can be found in the ornithological journals, particularly in *Bird-Banding* and *Vogelzug*. I have quoted all these figures merely to show that the enormous amount of similar evidence which has been published by the bird-banders is, unfortunately, useless for our purpose.

Sexual dimorphism: Another source of error in a study of the tertiary sex ratio in birds lies in their sexual dimorphism. The males of most species of birds are very much more conspicuous than the females. They are often more brightly colored, they sing and display, and, in the

case of territorial species, they are apt to inspect or even attack intruders. It is, therefore, not at all surprising that males predominate in random collections of birds. The great body of the figures compiled by Pelseneer (1926) is based on such collections and consequently useless for our purposes. The best proof for the fallacy of this method is given by the fact that museum collections always contain more adult males of the weaver birds (*Euplectes hordeacea* and *franciscana*) than females, although it is well known that in these species the females outnumber the males at least 2:1. Even in the species in which male and female are similar in coloration there is often a decided difference in behavior which may lead to error.

SEX RATIO AND LIFE HISTORY

Many ornithologists have failed to understand that the sex ratios in different families and even genera and species of birds are frequently quite different. For this reason it is wrong and illogical to say: The males outnumber the females among birds, or *vice versa*. Sound conclusions can only be reached if each group of birds is studied separately. A particular attraction is given to the study of the *tertiary sex ratio* in birds, because it is frequently correlated with some unusual mating behavior. It is, therefore, advisable to say a few words about pair formation in birds and to classify the occurrence of unusual sex ratios according to the pairing behavior in such species.

Birds are, as a rule, monogamous, at least for the duration of one brood. Occasionally, however, polygamy occurs, that is, several females settle in the domain or territory of one male and mate with him. In contradistinction we find polyandry in some other genera in which one female has several "husbands" who may take over a good share of the duties of incubation and raising of the young. Finally, we have a number of cases where no tie is formed by the sex partners, who separate completely after fertilization has been accomplished. This might be called "non-pairing."

SURPLUS OF MALES

Monogamous species: Before we mention any of the species with very unequal sex ratios we might examine a monogamous species in which the number of males approximate that of the females. Fortunately there is available a very excellent and reliable study on such a species. M. M. Nice's (1937) study of a population of the song sparrow (*Melospiza melodia*) on a forty-acre tract at Interpont near Columbus, Ohio, has the advantage that the author had individually marked nearly every bird in this area and knew its entire history. It seems unlikely that the accuracy of this study of a wild bird population will soon be surpassed and it is therefore worth while to quote some of her figures (*l. c.*, Table XXIV):

ADULT SONG SPARROWS PRESENT AT INTERPONT AT THE BEGINNING (APRIL 6) AND DURING THE LATTER PART (JUNE) OF THE BREEDING SEASON

	April 6		June		Loss in per cent. of April population	
	♂	♀	♂	♀	♂	♀
1930	30	30	27	25	10.0	16.7
1931	41	41	36	34	12.2	17.1
1932	69	65	61	51	11.6	21.5
1933	44	41	38	31	13.6	24.4
1934	29	25	23	16	20.7	36.0
1935	25	25	20	16	20.0	36.0
Total for 6 years.....	238	227	205	173	13.9	23.8
First 3 years	140	136	124	110	11.4	19.1
Last 3 years	98	91	81	63	17.4	30.8

The first 3 years may be considered as representing normal conditions. During the last 3 years the habitat was disturbed and partly destroyed, resulting in a reduction of the population and an increased exposure to enemies. The consequence is higher mortality, particularly of the females, which in this species are more vulnerable to predation.

THE FLUCTUATION OF THE SEX RATIO (♂ PER 100 ♀)

	Males in April	Males in June
1930	100	108
1931	100	106
1932	106	120
1933	107	123
1934	116	144
1935	100	125
Average for 6 years.....	105	118
First 3 years	103	113
Last 3 years	108	129

Summarizing these figures, we can say that the sex ratio of this song sparrow population was nearly balanced at the beginning of the breeding season, particularly during the three years when the habitat was undisturbed. Heavy losses to the incubating females, however, caused a decided rise of the ratio, to a maximum of 144 in June, 1934. It is probable that the heavier losses of the territory proclaiming males in the spring account for the approximate balancing of the sex ratio in every subsequent spring.

It is the opinion of most field ornithologists that among many song birds the males outnumber the females by about 10-20 per cent. To prove such a contention involves so much work that it is rarely undertaken. It requires not only that the territory of each male be determined but also that each female and nest, respectively, be located. Only few species or genera lend themselves to such a study. In the European genus *Phylloscopus* (wood warblers) it has been proved by several authors for at least three species. H. v. Treuenfels (1937) found in a small wood in northern Germany that twelve of thirty-five males of *Phylloscopus sibilatrix* did not find a female. This indicates a sex ratio of 1.52 ♂ per female. Price (1935) found that in two populations of chiff-chaffs (*Ph. collybita*) of 63 and 42 males, 25 and 14 remained unmated (1.66 ♂ or 1.50 ♂ per female). In the same two tracts of woodland the numbers of male willow warblers (*Ph. trochilus*) were 90 and 53, of which 18 and 23 remained unmated (1.25 ♂ or 1.77 ♂ per female). Similar figures have been reported by other authors for the chaffinch (*Fringilla*), warblers (*Sylvia*, *Acrocephalus*), robins (*Rubecula*) and other species. Since there is no evidence in these species of unmated females, it is reasonable to conclude that these figures actually represent the proportions of sexes in these populations.

Hicks (1934) found among 2,522 individuals of the starling (*Sturnus vulgaris*) trapped in their winter quarters in Ohio that 1,714, or 67.9 per cent., were males. The sex ratio changed as follows from month to month:

Beginning of winter	December	234 ♂ : 100 ♀
Midwinter	{ January	180 ♂ : 100 ♀
	{ February	171 ♂ : 100 ♀
End of winter	March	230 ♂ : 100 ♀

The fact that the sex ratio stayed high throughout the winter (notwithstanding some variation) is one of Hicks's principal reasons for believing in the actual existence of an unequal sex ratio in this species. Kluijver (1935) finds a preponderance of males also in Dutch starlings, even in breeding populations.

In the American bob-white quail (*Colinus virginianus*) exact records are available in several eastern and southern states (Stoddard, 1932). Among 19,423 birds shot in Georgia and Florida there were 53.3 per cent. males (114 ♂ : 100 ♀). Among 10,707 quails shot at ten localities of five states over a period of 28 years there were 53.0-58.0 per cent. males. Many other observations, some of them based on equally large figures, support the contention of a ratio of 112-130 males to 100 females. Unfortunately, there are no data available of the sex ratio of freshly hatched young, but some figures indicate a higher post-natal mortality and consequently shorter average life of the female.

Some of the most remarkable cases of an unequal sex ratio seem to occur in the family of the honey-eaters (Meliphagidae). The earliest reference to this condition seems to have been made by Stresemann (1928) in regard to the genus *Myzomela*. This genus, comprising about a score of the species, is restricted to the Australian region and reaches its highest diversity on New Guinea. Most species are strongly dimorphic, with the males decidedly more vividly colored, but males and females usually feed together in little parties in flowering trees. The males have a rather inconspicuous song.

Ordinarily I would hesitate to pay much attention to the proportion of sexes among specimens in museum collections, but in this genus the evidence is so uniform and so overwhelming that I want to record it in detail. To make the case more convincing, it may be mentioned that

it has been fully substantiated by my own observations during two years of collecting in New Guinea and the Solomon Islands and also by the experiences of other observers. L. Macmillan, who has been studying and collecting the birds of the New Hebrides for years and has given special attention to the matter of sex ratio, writes me on November 16, 1937: "The females of *Lichmera* are outnumbered by the males at least 10:1, just as in *Myzomela*. T. H. Harrison and myself found this so on Malekula and I found it so on Erromanga and also here in Mare (Loyalty Islands)."

The Sepik Expedition collected the following number of males and females of the various species (Stresemann, 1923):

<i>Myzomela eques</i> : 30 ♂, 5 ♀	85.7 per cent. ♂
<i>Myzomela cruentata</i> : 28 ♂, 2 ♀	93.3 " " ♂
<i>Myzomela nigrita</i> : 16 ♂, 13 ♀	55.2 " " ♂
<i>Myzomela rosenbergi</i> : 16 ♂, 6 ♀	72.7 " " ♂

The richest material, with which to check the sex ratio in *Myzomela*, was probably collected by the Whitney South Sea Expedition.

Myzomela jugularis (from 42 islands, covering all the months of the year except March, April and May)—Fiji Islands

78 ♂ ad., 35 ♂ imm., 18 ♀ ad., 6 ♀ imm.—82.5 per cent. ♂

Myzomela cardinalis chermesina—Rotumah Island

16 ♂ ad., 12 ♂ imm., 8 ♀ ad., 7 ♀ imm.—65.1 per cent. ♂

Myzomela cardinalis nigriventris—Samoa

60 ♂ ad., 3 ♂ imm., 7 ♀ ad., 6 ♀ imm.—82.9 per cent. ♂

Myzomela cardinalis tenuis—New Hebrides

73 ♂ ad., 34 ♂ imm., 24 ♀ ad., and imm.—81.7 per cent. ♂

Myzomela cardinalis sanctaecrucis—Santa Cruz Islands

58 ♂ ad., 5 ♂ imm., 14 ♀—81.8 per cent. ♂

Myzomela cardinalis sanfordi—Rennell Islands

18 ♂ ad., 2 ♂ imm., 5 ♀—80.0 per cent. ♂

Myzomela cardinalis pulcherrima—San Cristobal

10 ♂ ad., 1 ♂ imm., 5 ♀ ad.—68.8 per cent. ♂

Myzomela cardinalis malaitae—Malaita, Solomon Islands

34 ♂ ad., 13 ♂ imm., 12 ♀—79.7 per cent. ♂

(For further details about these species, see Mayr, 1932.)

I may add the percentage of males of some other species of the genus for which adequate material is available: *Myzomela lafargei*: 72 per cent.; *M. melanocephala*: 70.7

per cent.; *M. eichhorni*: 69.6 per cent.; *M. nigrata tris-trami*: 61.8 per cent.; *M. cardinalis rubrata*: 52.8 per cent.; *M. cardinalis saffordi*: 75 per cent.; *M. cardinalis major*: 71.4 per cent.; *M. cardinalis dichromata*: 51.1 per cent.; *M. cardinalis kobayashi*: 70.35 per cent. This list could be greatly enlarged.

It is difficult to interpret these figures. The easiest explanation would be to say that the collector picked out the brightly colored and conspicuous males and neglected the collecting of females. There are two objections to this explanation. The first is that there are many other genera with equally or even more pronounced sexual dimorphism, but no such lopsided sex ratios are found in collections of these genera. The second objection is that in many cases there are in the collection more dull-colored immature males (which are in some of the species even more plainly colored than the females) than adult and immature females combined.

It is nevertheless possible that a correlation exists between sexual dimorphism and sex ratio, since there seems to be the smallest surplus of males in the species with the least developed sexual dimorphism. There is nothing known of the life history of these birds which would help to explain this sex ratio. They seem to be monogamous. Unfortunately, they are tropical birds, with only two young, and it will be difficult to gather sufficient data on the secondary sex ratio.

The only other genus of this family in which the males outnumber the females (by about 8 or 9:1) is *Lichmera* (formerly *Stigmatops*). Remarkable in this case is the fact that in most of the species of this genus there is practically no sexual dimorphism, except for size.

A. Skutch reports (1935) of the Central American bush-tit (*Psaltiriparus melanotis*) that the males outnumber the females about 4 to 6:1, which leads to the interesting habit that the unmated bachelor males help the mated pairs to feed the young. At three nests there were 1, 1 and 3 extra males sharing the duty of feeding the young. Skutch

reports that the twelve young which fledged from the three nests were all males. The sex was, however, not determined by dissection and it is possible that the young female resembles the male rather than the adult female.

Following these typically monogamous species, I shall treat some others of which the sexual relationship might best be classified as monogamy, although they are not quite typical. (See below, p. 172, for the cowbird.)

In the ducks (Anatidae) a preponderance of males has been recorded by a number of authors. McIlhenny (1937b) quotes the following sex ratios (among others) of birds trapped in their winter quarters at Avery Island, La.:

Ring-necked duck (<i>Nyroca collaris</i>)	961 ♂, 286 ♀ (335 ♂ : 100 ♀)
American pintail (<i>Dafila a. tzitzihua</i>)	2780 ♂, 1413 ♀ (197 ♂ : 100 ♀)
Blue-winged teal (<i>Querquedula discors</i>)	1318 ♂, 752 ♀ (175 ♂ : 100 ♀)

Similar figures have been quoted in Lincoln (1932) from the enormous material gathered by the U. S. Biological Survey.

Frieling (1934) analyzes the field observations made in Germany of 21,764 ducks belonging to 10 different species and finds the following number of males per 100 females:

Spatula clypeata, 178; *Bucephala clangula*, 170; *Nyroca ferina*, 160; *Anas penelope*, 145; *Nyroca fuligula*, 137; *Anas platyrhynchos*, 130; *Anas querquedula*, 127; *Anas acuta*, 123; *Anas crecca*, 118; *Anas strepera*, 112.

These figures indicate less of a disproportion than those of the banders quoted above. A monthly analysis indicates that in some of the species the females prevail in certain months and differ from the males in migration time, routes and winter quarters. Considering all the evidence together the preponderance of males has been established beyond doubt.

The high sex ratio of ducks has been confirmed by an analysis of a breeding population (Furniss, 1935). It would be highly interesting to determine the secondary sex ratio of the domestic duck.

Polyandrous species: Polyandry, that is the mating of

several males with one female, occurs in birds only rarely. It is restricted to those species (except for the above-described occurrence of the pseudo-polyandry in one species of *Psaltiriparus*) in which the female is the more active participant in the courtship ceremonies and the male assumes the duties of incubation. Even in these species there is not always a surplus of males, as has been pointed out for *Phalaropus* by Tinbergen (1936). In fact, in the case of the Wilson's phalarope (*Steganopus tricolor*) Wetmore (1926) believes, on the contrary, in a surplus of females. Polyandry, of course, means that there is a surplus of males, but it is rather difficult to find reliable figures, since most polyandrous species live in the tropics.

The polyandrous button-quails (*Turnix*) live in the densest grass, and exact counts of males and females are impossible. Captivity observations indicate that one female may have as many as eight or nine males (Stresemann, 1928).

The painted snipe (*Rostratula*) is also known to be polyandrous. Pitman (1912) found in India in an isolated nesting colony 4 females with 12 males, and Stuart Baker (1935) found one female with 4 males at a different locality. This would suggest a proportion of 3-4♂:1♀, but more material must be gathered to substantiate these figures.

Beebe (1925) estimates that in the tinamou (*Crypturus variegatus*) there were about 4 males to every female. In the population in British Guiana which was studied by him, there were 32♂ and 8♀.

SURPLUS OF FEMALES

Monogamous species: A surplus of females in normally monogamous species has been recorded only from one order of birds, that of the hawks (*Accipiters*). Among 291 goshawks that were killed on migration there were 110♂ and 181♀ (Wood, 1938). This might be explained by the greater migratory urge of the females, but it is supported by a few data on the secondary sex ratio in

the European sparrowhawk (*A. nisus*). Gunn (1912) examined two nests in England and found in one nest 1♂, 5♀, in the other 2♂, 4♀. Maniquet (1927) examined three nests in France and found only four males among the fifteen young. The total sex ratio of the five broods is 7♂ and 20♀, or about 3 females per male. There is, however, also some conflicting evidence, particularly in other genera of hawks, and it is advisable to gather more material before one speculates on the possible reason for this surplus of females (see also Mayr (1938)).

Polygamous species: More and more evidence has accumulated in recent years to show that polygyny is not as rare in birds as formerly believed. It occasionally occurs as an exceptional condition even in species in which there is normally a surplus of males as in the song sparrow (Nice, 1937). But in addition to these exceptional cases, which have been reported from a number of families of birds, polygyny is a normal condition in certain species of at least seven different families of birds. The bond between the male and his females is sometimes very weak and it would probably be more correct to classify such species as "non-pairing."

Only one case of polygyny is known in the heron family (Ardeidae). Zimmermann (1929) showed that one male of the European bittern (*Botaurus stellaris*) may have several females and this observation has been confirmed by several other ornithologists (J. Vincent, U. von Sanden). It is of course impossible to ascertain the exact sex ratio in this secretive marsh bird.

The majority of the gallinaceous birds seem to have a fairly even sex ratio. The common fowl, which is polygamous in its domesticated state, is a descendant of the jungle fowl, which according to some observers (but not according to others) is monogamous. It is a general statement in the ornithological literature that the peafowl (*Pavo cristatus*) is polygamous. Several observers state that they have seen males accompanied by little harems of 5 to 6 hens. These field observations do not harmonize

with the experiences of a well-known breeder of this species, who writes me: "I can tell you absolutely that over a period of many years in breeding peafowl in confinement, the numbers of males and females are just about equal. . . . This covers and is true of both the Blue and the Green birds, as well as the varieties produced in domestication: Black-winged, White and Pied" (C. L. Sibley, *in litt.*). There is some evidence to suggest a surplus of females in certain genera of the Tetraonidae, as for example in the black cock (*Lyrurus tetrix*). In the big flight of the sharp-tailed grouse (*Pedioecetes phasianellus*) in 1932 there were 48♀ and 17♂♂ in 65 killed specimens. But nothing is known about the sex ratio on the breeding grounds (Snyder, 1935).

In the family of the bustards (Otidæ) there is also some evidence for a surplus of females. I have, however, been unable to find any reliable counts.

The females also greatly outnumber the males in many genera of hummingbirds (Trochilidae). Nicholson (1931) writes of the Guiana king hummingbird (*Topaza p. pella*): "The dullish green females and immature males would be seen a hundred times or more for each glimpse of the old male." The apparent sex ratio in this population was 8♂: 30♀, although various factors made it difficult to ascertain whether or not this was numerically correct. The fact that immature males resemble the females and that the males do not share the duties of incubation and raising of the young makes exact counts impossible. On the other hand, each male has its definite territory and lookout posts which helps to determine their actual number in a given region.

These are the only cases among Nonpasseres that have come to my attention. Among the songbirds polygyny occurs more frequently. Its occurrence is, again, restricted to certain families. In the family of the buntings (Emberizidae) most species are strictly monogamous. The exceptions that occur in the song sparrow have been mentioned above. Some cases of polygamy have also been

reported for the white-crowned sparrow (*Zonotrichia l. nuttalli*) (Blanchard, 1936), but the only species in which polygyny occurs regularly is the corn bunting (*Emberiza (Miliaria) calandra*). Ryves (1934) found in a first rough survey, in 1932, 27 nests in the territory of 16 males, which indicates a sex ratio of 100♂:169♀. In a somewhat more thorough investigation in 1933 he found 45 nests with females in the territory of 24 males, indicating a sex ratio of 100♂:187.5♀. Although the males are very conspicuous, the females are shy and retiring and it seemed probable that some of them had been overlooked. Ryves therefore contented himself in 1934 with a smaller area but covered it very thoroughly. In this area there were 15♂:51♀. This means a sex ratio of 100♂:340♀. All the 1934 males were polygamous, four had two females each, seven had three females, two had four females and two had seven females each. There is no reason to doubt these figures, since each male and each female was held under observation for a considerable period.

The family of birds in which polygyny seems to occur most often is that of the weaver birds (Ploceidae), and this has been known for many years.

W. W. Bowen (1926) observed in the Sudan two small colonies of the bishop bird (*Pyromelana franciscana*) which are sufficiently isolated to make his observations reliable. One of these colonies consisted of five females with a single male, which jealously guarded his territory against the intrusions of other males. In the other colony the single male had apparently a dozen females. Probably the most exact observations of any such species are those of David Lack (1935) on the crimson-crowned bishop bird (*Euplectes hordeacea hordeacea*) of East Africa. Of five males that were held under observation for several weeks, one had one female, two had two females, one had three, and one three or four. Polygyny for the same species and also for *Euplectes nigroventris* (1♂:3-4♀) is also reported by Vaughan (1930). The observations of Ali (1931) indicate a surplus of females in the Indian weaver

bird (*Ploceus philippinus*). No actual figures are given, but a male usually has two females, sometimes three, and it seems that the males are outnumbered by the females about 2:1.

The most interesting family for a study of sex ratios is probably that of the Icteridae (American blackbirds) because it contains some genera with an equal sex ratio, some with a surplus of males and some with a surplus of females. An equal sex ratio occurs probably in the majority of the species; there is evidence available to support it in the case of the bronzed grackle (*Quiscalus aeneus*) (Snyder, 1937), the Brewer's blackbird (*Euphagus cyanocephalus*) (Linsdale, 1938) and the Baltimore oriole (*Icterus galbula*) (own observations).

A surplus of males occurs only rarely in this family. It has been claimed both for the shiny cowbird (*Molothrus bonariensis*) and the common cowbird (*M. ater*) (Friedmann, 1929). Two or three males per female are said to exist, but only positive evidence seems to be banding record of 1,902♂ and 769♀ (2.47♂ per ♀) (McIlhenny, 1937b). There is considerable doubt about the sex ratio of the red-winged blackbird (*Agelaius phoeniceus*). Cases of polygamy in this species have been reported by several authors (Allen, 1914, Linsdale, 1938), but among trapped birds males outnumbered females about 3 to 1 (McIlhenny, 1937b) and more males than females are also found to occur among the young in the nest (Herman, 1938).

Polygyny is firmly established in three species of Icteridae. Chapman (1928) found, in 1926, in an isolated colony of Wagler's oropendola (*Zarhynchus wagleri*) on Barro Colorado, Panama, six or seven males and 39 females and in 1927 five or six males and 29 females indicating about 5 ♀ per male. Polygyny has also been observed in the yellow-headed blackbird (*Xanthocephalus xanthocephalus*) (Linsdale, 1938, Ammann, unpublished) with about 2 females per male. In the boat-tailed grackle (*Cassidix mexicanus*) not only the tertiary sex ratio has been studied but also the secondary. McIlhenny (1937a)

found a great preponderance of females in several colonies of this species at Avery Island, Louisiana. It is rather difficult to obtain reliable figures on the sex ratio of this species, which is not pair-forming, but among 874 feeding birds that were trapped and banded in 1935 there were 271♂ and 603♀, and among 974 birds trapped in 1936 there were 338♂ and 636♀, which corresponds to 31.0 per cent. or 34.7 per cent. ♂.

In 89 nests in which the young reached the age at which sex could be definitely determined, the following sex ratios prevailed:

Secondary sex ratio:				Primary sex ratio:			
1 nest	contained	2 ♂ only		3 nests	2 ♂ and	1 ♀	
8 nests	"	1 ♂ "		28 "	1 ♂ "	2 ♀	
3 "	"	2 ♂ and	1 ♀	6 "	0 ♂ "	3 ♀	
26 "	"	1 ♂ "	1 ♀	—	—	—	—
28 "	"	1 ♂ "	2 ♀	37 "	34 ♂ "	77 ♀	
6 "	"		3 ♀ only				
15 "	"		2 ♀ "				
2 "	"		1 ♀ "				
—							
89 "	"	70 ♂ "	135 ♀				

The secondary sex ratio is thus 34.1 per cent. ♂ and 65.9 per cent. ♀, and the primary sex ratio 30.6 per cent. ♂ and 69.4 per cent. ♀, fluctuating approximately within the same limits as the tertiary sex ratio.

DISCUSSION

Three questions present themselves to the student of the above-given evidence. First: What are the changes of sex ratio between the time of fertilization (primary sex ratio) and adulthood (tertiary sex ratio) and what factors cause them? Second: How can the existence of an unequal primary sex ratio be reconciled with our present knowledge of the genetics of sex determination in vertebrates? And third: What is the biological significance of uneven sex ratios?

To answer the first question, we must analyze all the known cases where (primary), secondary and tertiary sex ratios of one species are known. In the domestic pigeon

Cole and Kirkpatrick (1915) found a secondary sex ratio of 105♂:100♀ and recorded that there was, aside from some minor fluctuations, no significant change of the sex ratio with advancing age. In the domestic fowl the prenatal (egg stage) mortality of the females is significantly, but very slightly, higher than in the males. A really high sex-linked lethality occurs, so far as I know, only in species and genus hybrids and in some closely inbred domestic varieties.

There is little published evidence on mortality in the eggs of wild birds. The few data which I have been able to gather indicate that completely sterile eggs occur not uncommonly, but that embryo mortality in the egg due to lethal factors and not due to chilling or other environmental factors is quite rare. However, no definite figures are available. As a matter of fact, even in the domestic fowl, there are only few sex-linked lethals known. There is every reason to believe that lethals are of no importance for the explanation of strongly unbalanced sex ratios in birds.

We know next to nothing about internal physiological factors that might influence sex ratios in birds. It is possible that the males have a greater longevity in certain species, on account of greater resistance to diseases and the rigors of the environment, but the available data do not permit sound conclusions. Spontaneous sex reversal (masculinization) has been observed in the domestic fowl in exceptional cases, but this phenomenon is unlikely to be of major importance. A complete determination of the secondary sex characters by sex hormones is, according to more recent research, probably rather an exception than the rule. Sexual dimorphism is apparently determined genetically in most species of birds.

Environmental factors are in many species of birds largely responsible for the difference between secondary and tertiary sex ratio, and there is no question that these factors are much more important than physiological factors; furthermore, they are more easily investigated.

They principally consist of a differential vulnerability of male and female to certain dangers. As has been stated above (p. 162), male song sparrows suffer the greatest losses during the spring period of territory establishment and courtship, while female song sparrows are most vulnerable during the period of incubation. A similar high mortality of females during the breeding season occurs probably in all the species in which the female carries the whole burden of incubation, particularly if the species is ground nesting. The above quoted lack of females among wood warblers (*Phylloscopus*) and ducks might possibly be explained on this basis.

Even if we take all these factors (lethal, physiological and environmental) into consideration, many cases remain in which there is little doubt about an actually unequal primary sex ratio (*Psaltiriparus*, *Myzomela*, *Accipiter*, *Ploceidae* and *Icteridae*).

The only species in which actual figures are available (see p. 172) is the boat-tailed grackle (*Cassidix mexicanus*). McIlhenny (1937a) reports a primary sex ratio (only complete clutches counted!) of 30.6 per cent. ♂ and 69.4 per cent. ♀, a secondary sex ratio of 34.1 per cent. ♂ and 65.9 per cent. ♀, and tertiary sex ratios of 31.0 per cent. ♂ and 69.0 per cent. ♀ (1935), and 34.7 per cent. ♂ and 65.3 per cent. ♀ (1936). These figures show not only that the primary sex ratio in this species is very uneven, but they also indicate that no major shift in the sex ratio occurs during the lifetime. The variation of males between 30 and 35 per cent. is probably due to the small numbers.

The final conclusion is that in birds the primary sex ratio is frequently very unequal, just as Crew (1937) had maintained. This leads us to our second question: How can the existence of an unequal primary sex ratio be reconciled with our present knowledge of the genetics of sex determination in vertebrates?

Our knowledge of the chromosomes of birds has been computed recently by Miller (1938), who records that the sex inheritance follows the wo (♀), ww (♂) scheme in the

gallinaceous birds and in the Passeres, the only two orders of birds in which modern investigations are available. In other words, so far as we know, the males are homozygous and the females heterozygous for the sex factor, and we should expect a primary sex ratio of 50 per cent. ♂ and 50 per cent. ♀. The fact that so many exceptions to this ideal ratio occur indicates that some additional factors combine with *w* in the sex determination. Crew (1937) formulates this as follows: "... there should be genes which affect the functioning of the heterogametic mechanism." The differences in the sex ratios of different strains of canaries reported by Heape (1907) also suggest the presence of such modifying factors. Such genes have been described for several species of *Drosophila*. In the case of birds, they probably affect the oocytes in the ovary prior to ovulation. The occurrence of strong and weak sex factors (as in *Lymantria*) is less probable, since we would expect in this case intersexes which in birds are almost unknown.

Friedmann's (1927) attempt to correlate unequal sex ratios with the testicular asymmetry that is so common in birds does not seem very successful. Not only is testicular asymmetry known from many species with equal sex ratio, but furthermore the sex-determining mechanism is unlikely to exist in the males, if the female is the heterozygous sex. This, of course, has not yet been established beyond doubt, since, as stated above, the number of investigations is still small and restricted to a small percentage of the known families of birds. There is an urgent need for more cytological and genetic investigations on the sex determination in birds in order to gain a more secure foundation for an interpretation of the phenomena observed in nature. A full knowledge of the facts may force us to a more physiological interpretation of sex determination, and Riddle's work on these problems may appear in a new light.

Commenting on the significance of unequal sex ratios, Crew (1937: 554) comes to the conclusion that they are

correlated with sex-linked mortality and that the overproduction of one sex serves to establish a reserve against such mortality. It seems to me that this conclusion is much too restricted and that unequal primary sex ratios may also occur in connection with an increased demand for one sex during adulthood, in all species with special habits such as polygyny, polyandry, etc. Unquestionably sex determination in vertebrates is a good deal more complicated than is generally recognized.

The writer wishes to thank Professors L. C. Dunn, W. Landauer and A. H. Miller and Mrs. M. M. Nice for reading the manuscript and for many valuable suggestions.

SUMMARY

(1) The principal purpose of this paper is to show that in birds a great deal of well-documented evidence exists proving the occurrence of strongly uneven sex ratios.

(2) The sex ratio may be high or low, favoring the male or the female sex.

(3) The evidence points to the existence of this unbalanced condition already in the primary sex ratio, although physiological and environmental factors may modify it during prenatal and postnatal life.

(4) In nearly all well-studied cases unequal sex ratios have been found to be correlated with peculiarities in the life history of the birds.

(5) The study of the cytology and genetics of sex determination in birds is a promising and practically untouched field.

LITERATURE CITED

- Ali, S.
1931. *Jour. Bombay Nat. Hist. Soc.*, 34: 947.
Allen, A. A.
1914. *Abstr. Proc. Linn. Soc. N. Y.*, 24-25: 92.
Baker, Stuart
1935. *Nidif. Birds Ind. Empire*, 4: 326.
Beebe, W.
1925. *Zoologica, N. Y.*, 6: 195.
Blanchard, B. D.
1936. *Condor*, 38: 146-150.

- Bowen, W. W.
1926. *Ibis*: 441-444.
- Byerley, T. C. and M. A. Jull
1935. *Poultry Sci.*, 14: 217-220.
- Chapman, F. M.
1928. *Bull. Amer. Mus. Nat. Hist.*, 58: 135.
- Cole, L. J. and F. Kirkpatrick
1915. *Agr. Exp. Sta. Rhode Is. Bull.*, No. 162: 463-512.
- Crew, F. A. E.
1937. *AMER. NATURALIST*, 71: 529-559.
- Drost, R.
1935. *Vogelzug*, 6: 177-182.
- Friedmann, H.
1927. *Biol. Bull.*, 52: 197-207.
1929. "The Cowbird": 77, 173.
- Frieling, H.
1934. *Vogelzug*, 5: 109-115.
- Furniss, O. C.
1935. *Wilson Bull.*, 47: 277.
- Goethe, F.
1937. *Jour. Ornith.*, 85: 67.
- Groebbels, F.
1937. "Der Vogel," II: 104-106.
- Gunn, T. E.
1912. *Proc. Zool. Soc. London*: 67.
- Heape, W.
1907. *Proc. Cambridge Phil. Soc.*, 14: 201-205.
- Heinroth, O.
1912. *Orn. Monatsber.*, 20: 148.
- Herman, C. M.
1938. *Bird-Banding*, 9: 92-93.
- Heydweiller, M.
1936. *Bird-Banding*, 7: 65-67.
- Hicks, L. E.
1934. *Bird-Banding*, 5: 104-107.
- Kluijver, H. N.
1935. *Ardea*, 24: 159.
- Lack, D.
1935. *Ibis*: 824.
- Liebe, K. Th.
1894. *Orn. Monatsber.*, 19: 77.
- Lincoln, F. C.
1932. *Amer. Game*: 16.
- Linsdale, J.
1938. *Amer. Midland Naturalist*, 19: 128, 140.
- Lucanus, F. von
1917. *Jour. Ornith.*, 65 II: 166.
- Maniquet, E.
1927. *Rev. Franc. Ornith.*: 423.

- Mayr, E.
1932. *Amer. Mus. Novit.*, No. 516: 17-30.
1938. *Auk*, 55: 522-523.
- McDowell, E. C. and E. M. Lord
1925. *Anat. Rec.*, 31: 143-148.
- McIlhenny, I. E.
1937a. *Auk*, 54: 291.
1937b. *Bird-Banding*, 8: 117-121.
- Miller, R. A.
1938. *Anat. Rec.*, 70: 155-190.
- Nice, M. M.
1937. *Trans. Linn. Soc. N. Y.*, 4: 29, 88-90, 173.
- Nicholson, E. M.
1931. *Ibis*: 535.
- Pelseneer, P.
1926. *Mem. Acad. R. Belg.*, oct. coll., 8 (2), fasc. 11: 69-79.
- Pitman, C. R. S.
1912. *Jour. Bombay Nat. Hist. Soc.*, 21: 666.
- Price, M. P.
1935. *Brit. Birds*, 29: 158-166.
- Ryves, B. H.
1934. *Brit. Birds*, 28: 2-26, 154-164.
- Skutch, A.
1935. *Auk*, 52: 267.
- Snyder, L. L.
1935. *Univ. Toronto Stud.*, Biol. Ser., No. 40: 23.
1937. *Canad. Field Nat.*, 51: 37.
- Stoddard, H. L.
1932. "The Bobwhite Quail," p. 89-95.
- Stresemann, E.
1923. *Arch. Naturg.*, 89 A7: 49-51.
1928. *Aves*, in: *Kükenthal Handb. Zool.*, VII 2: 315, 378.
- Tinbergen, N.
1935. *Ardea*, 24: 28.
- Treuenfels, H. von
1937. *Jour. Ornith.*, 85: 607.
- Vaughan, J. H.
1930. *Ibis*: 44-45.
- Wetmore, A.
1926. "The Migration of Birds": 167.
- Wood, M.
1938. *Auk*, 55: 124.
- Zimmermann, R.
1929. *Jour. Ornith.*, Suppl. II: 263.

SHORTER ARTICLES AND DISCUSSION
CHROMOSOME ASSOCIATION IN *MESOSTOMA*
EHRENBERGII (Focke) Schmidt

Mesostoma ehrenbergii of the order Rhabdocoela was reported from Europe by Focke in 1836 and first found in America by Woodworth in 1897. Graff (1913) states that it has been reported from numerous places in Europe and Asia, from Kansas, Michigan, Ohio, Illinois and New York in the United States, and from Trinidad. The chromosome number of the European *M. ehrenbergii* is five haploid and ten diploid according to Luther (1904), Bresslau (1904) and Voss (1914). The figures of meiotic anaphase I given by Voss, and Bresslau's drawings of the first cleavage show clearly that the European form has five pairs of chromosomes with approximately median centromeres.

During the fall of 1937 we obtained specimens of *M. ehrenbergii* collected from the Genesee River between the lower falls and Lake Ontario. This race appears to be structurally the same as the European form but different in chromosome number, chromosome morphology and probably in chromosome behavior. The animals from the Genesee River have the largest Turbellarian chromosomes reported up to this time. Each pair of chromosomes can be distinguished morphologically from the others. One of these pairs is never associated at meiotic metaphase. The eleven individuals which have been examined have the same chromosome number, morphology and peculiar meiotic behavior.

Eight chromosomes are found at mitotic metaphase (Fig. 1):

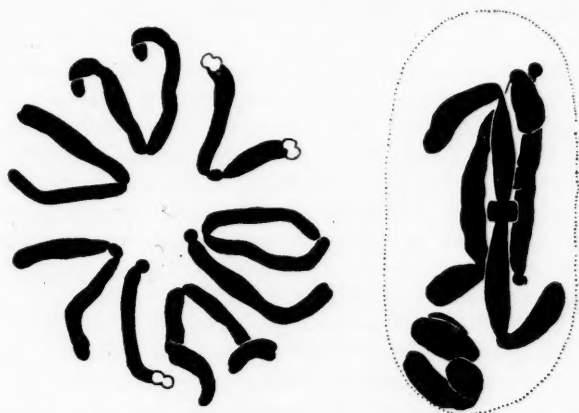
(1) Two chromosomes have subterminal centromeres and are approximately $14\ \mu$ long.

(2) Two have nearly median centromeres and are approximately $17\ \mu$ long.

(3) Two are from $2-3\ \mu$ longer than those of pair 2 and have a second constriction about $1\ \mu$ from the nearly median centric constriction. The two constrictions at metaphase are indistinguishable.

(4) Two chromosomes have nearly median centromeres and are approximately $27\ \mu$ long.

The chromosomes are approximately $1.2\ \mu$ in diameter and are usually distributed on the spindle with their long arms reaching into the cytoplasm. All the chromosomes show relic coiling, which persists in some of them until anaphase.



FIGS. 1 and 2. Chromosomes of *M. ehrenbergii*. $\times 2500$. 1. Mitotic metaphase. 2. First meiotic metaphase.

The meiotic prophase chromosomes are crowded in the small nuclei and with the methods employed so far are rarely fixed in a satisfactory manner. As the nuclear membrane of the primary spermatocyte disappears, the cell becomes elongated, presumably correlated with the formation of a long and narrow spindle. Three rod bivalents are usually oriented on the spindle at metaphase I and two univalents remain in the cytoplasm (Fig. 2). Although approximately one hundred cells have been studied at this stage in eleven individuals, no cell containing four bivalents has been seen. The two univalents are found at opposite ends of the cell, or in ca. 38 per cent. of the cells, at the same end. The uniformity of the situation and the presence of two univalents at the same end of the cell precludes the possibility that they result from precocious bivalent separation. The occurrence of univalents results in the formation of secondary spermatocytes which do not contain a uniform number of chromosomes. If these cells produce functional sperms, individuals which differ in the number of their chromosomes may be found.

The three bivalents can be readily identified. The members of the first pair of chromosomes which have subterminal centromeres are always associated. Either one, or in ca. 20 per cent. of the cells, two chiasmata are present in their long arms. When two occur, one is always terminal. The average chiasma frequency of this bivalent is 1.216.¹ One bivalent is attenuated near

¹ This and the data which follow are based on an analysis of sixty cells.

one or both centromeres in all the cells. A constriction, probably the centric constriction, is often seen in at least one of the free arms. This chromosome pair has an average chiasma frequency of 0.983. Approximately 70 per cent. of the chiasmata present are terminal. The arms of this pair are considerably shorter than the associated arms of the one previously described. Because of size and the presence of an attenuated region it is considered to be the third chromosome pair. The remaining bivalent is longer than the other two. It has an average chiasma frequency of 0.983. Over 30 per cent. of the chiasmata are terminal. It is undoubtedly the fourth pair of chromosomes.

Chromosomes "one" are always associated at metaphase I. Chromosomes "three" are found as univalents in one cell of the sixty selected at random, and chromosomes "four" as univalents in another. The first pair of chromosomes in one fifth of the cells has two chiasmata so only this proportion of cells has an average chiasma frequency of 4. Although four chiasmata are formed in a cell, the smallest bivalent contains two of them. If three are formed, the first chromosome pair, the attenuated bivalent and the long bivalent contain them (with the exception of one of the two cells which contain four univalents). In the one cell which contains only two chiasmata, the first pair of chromosomes and the third are the only chromosomes associated. It is clear that in the cells which contain three bivalents, the easily distinguishable first and fourth pairs are always associated. The third bivalent is always attenuated at one or two regions. If this attenuation is characteristic of a particular chromosome pair, *always the same chromosomes are unpaired in M. ehrenbergii at metaphase I.*

The attenuated bivalent has been considered to be the third pair of chromosomes because of its size and because the members of the third pair of chromosomes have a second constriction near their centromeres. The second constriction may be the region which becomes stretched into a slender thread at meiotic metaphase. It has been suggested that regions of chromosomes sometimes become drawn into thin threads by the stretching of the spindle. Either chromosome pair "two" or "three" because of its smaller size might be in the region of the spindle where the stretching action may be most effective. The members of the second pair of chromosomes have no second constriction near their centromeres and should be expected to behave like the first pair.

This pair, because it is often associated by chiasmata that are not terminal, is frequently oriented in the same general region of the spindle as the attenuated bivalent which usually has a terminal chiasma. Since the first pair of chromosomes has not been seen stretched into a thread, and an attenuated bivalent is always present in the cells which contain three pairs of chromosomes associated, there can be little doubt that the attenuated bivalent is always the third pair of chromosomes and that the members of the second pair are contracted less and never associated at meiotic metaphase.

Until a suitable technique is developed for the study of pachytene in *M. ehrenbergii*, we can not determine whether the situation here is due to asynapsis or failure of chiasma formation after normal pairing. Since the European form has ten diploid chromosomes and this form eight, the supposition that two chromosomes in the American *M. ehrenbergii* are without synaptic mates is an attractive one. It is not supported, however, by a study of the only other described species of *Mesostoma* in America. This species, *M. virginiana*, has eight chromosomes which regularly form four bivalents.

It can not be assumed that the unpaired chromosomes are paired at pachytene but are too short for the formation of chiasmata to occur because the shortest chromosome pair has the highest chiasma frequency. Arm length, however, may be a factor. The unpaired chromosomes are not the shortest in the complement, but they have the shortest arms. The third chromosomes appear to have slightly longer arms. Seventy-one per cent. of the chiasmata in this pair are terminal. The fourth chromosomes have arms of about equal length and approximately the same length as the long arm of the first chromosome. The fourth chromosomes have the same average number of chiasmata as the third pair, but only thirty-two per cent. of them are terminal. Its size may prevent sufficient association to assure a higher chiasma frequency.

It is probable that the arms of the second chromosomes are long enough for the formation of chiasmata to occur in the light of Mr. R. I. Bosman's unpublished work on the related flatworm *Gyratrix hermaphroditus*. This species has four diploid chromosomes. Two have subterminal centromeres and are rarely associated at meiotic metaphase. Two chromosomes have median centromeres. These measure approximately two times the length of the other pair and are associated by chiasmata which are local-

ized at the centromeres. When the chromosomes with subterminal centromeres are associated, chiasmata are usually but not always localized at the centromeres. Insufficient length alone can hardly explain the subterminal chromosomes being nearly always unpaired in *Gyatrix*.

The failure of chromosome association at meiotic metaphase has been shown to be the result of a recessive gene by Beadle (1930) and others and to environmental conditions by various workers. The effect in either case seems to be variable. The complete absence of association and nearly normal bivalent formation are often found in the same individual. In the eleven specimens of *M. ehrenbergii* we have seen, no cell containing all the chromosomes paired is present. The third pair of chromosomes is never associated. This peculiar situation to our knowledge has not been previously encountered.

A more detailed study of the chromosomes of the American species of *Mesostoma* will be reported elsewhere.

Since this article was accepted for publication, we have received a paper by A. Valkanov (Cytologische Untersuchungen über den Rhabdocoelen. Jahrbuch der Universität Sofia, Physico-Mathematische Fakultät, 34: 321-402, 1938) in which he describes the chromosome behavior in the European form of *M. ehrenbergii* and in the other species of Rhabdocoela. Valkanov's paper has not been translated but in his German summary he writes: "Während der Spermatogenese wird die parallele Konjugation noch im Pachitän gestört und durch eine späte Metasyndese, Amphimetasyndese oder durch einer völligen Isolation der homologen Chromosomen ersetzt. Bei *Mesostoma Ehrenbergii* ($2n=10$) bilden sich auf dieser Weise im Prophase der Reductionsteilung 3 Tetraden und 4 univalente Chromosomen, bei *M. lingua* ($2n=8$) bilden sich 4 Tetraden oder 3 Tetraden und 2 univalente Chromosomen, bei *M. sp. II* und *Rhyncomesostoma rostratum* bilden sich stets nur univalente Chromosomen."

The old world *M. ehrenbergii* which Valkanov has studied differs from the American *M. ehrenbergii* in chromosome morphology and number but the two forms do not seem unlike in the behavior of their chromosomes at the first meiotic division in testis tissue. Four chromosomes fail to associate in the form with ten chromosomes while two of the eight chromosomes are unpaired in our material.

UNIVERSITY OF VIRGINIA

LADLEY HUSTED
F. F. FERGUSON
M. A. STIREWALT

LITERATURE CITED

- Beadle, G. W.
1930. *Cornell Univ. Exp. Sta. Mem.*, 135.
- Bresslau, E.
1904. *Zeits. f. wiss. Zool.*, 76: 213-332.
- Graff, L. v.
1913. "Das Tierreich. Turbellaria II. Rhabdocoelida." Berlin.
- Luther, A.
1904. *Zeits. f. wiss. Zool.*, 76: 213-332.
- Voss, H. v.
1914. *Arch. f. Zellforschung*, 12: 159-194.

THE HINDRANCE TO GENE RECOMBINATION IMPOSED
BY LINKAGE: AN ESTIMATE OF ITS TOTAL
MAGNITUDE

STUDIES of hybridization in natural populations have shown (Riley, 1938; Delisle, 1937; Goodwin, 1937; Anderson and Hurbright, 1938; Anderson and Turrill, 1938) that the characters of the parental species tend to stay together in such populations. While this had been predicted (Anderson, 1936) from a consideration of the linkage of multiple factor characters with each other, the phenomenon is of such practical and theoretical importance as to deserve rigid mathematical exposition. The following paper attempts to estimate the hindrance to free recombination imposed upon hybrids by gene linkage alone. It does not consider the effect of such other restraints as pleiotropy, selective fertilization, zygotic elimination and gametic elimination.

It has been immediately apparent to those who have considered the question that linkage greatly reduces the chances of recombination. Jones (1920), for instance, has computed the chances of recombining favorable genes in maize. "Two factors in each chromosome so spaced as to have 10 per cent. breaks in the linkage with each other would necessitate 20^{20} individuals in the segregating generation to have an even chance of securing the one plant desired. This number of corn plants would require an area roughly 3,700,000,000,000 times the area of the United States."

The restraint of linkage, however, is not combined to frequencies. It also imposes severe restrictions upon the kinds of gene combinations which are possible with any frequency. When all the loci of a germ-plasm are considered this restriction is even greater than that imposed upon frequencies and runs into figures of astronomical magnitude. Some notion of this restriction may be gained by

considering recombination in a single cross-over segment of the germ-plasm. Let us take the simple case of a short chromosome in which there is regularly a single cross-over. Let us further suppose that in the two species, or races, which are to be crossed, there are ten pairs of gene differences within this chromosome. This seems a conservative number for a length of germ-plasm which might well be fifty units long genetically and made up of two hundred or more genes.

In the gametes of the first generation hybrid, as a result of four-strand crossing-over, one half of the gametes will have one crossed-over section in this chromosome and the other half will have none. The number of cross-overs per chromosome will be increased the same way in each generation; double cross-overs will not be possible until the F_2 generation forms its gametes, triple cross-overs until the F_3 , etc. In each generation one half the gametes will acquire an extra cross-over, one half will continue the previous number. The number of cross-overs per gamete and the proportions of each kind of gamete can therefore be obtained from expanding $(\frac{1}{2} + \frac{1}{2})^n$ where "n" equals the number of hybrid generations. For the ten gene pairs under consideration complete recombination can not be attained until gametes are produced in which all nine breaks between the original sets of ten differing gene pairs have occurred. To obtain such a gamete will require a minimum of nine hybrid generations, and even then these gametes may be expected only once in 2^9 (=512). It will require twice as many hybrid generations before gametes of this degree of recombination will be in the majority. The above figures have all been obtained on the hypothesis of random crossing-over along the chromosomes. Actually, of course, cross-overs would tend to recur in particular areas and thus greatly reduce the possibility of complete recombination.

A more precise estimate of the hindrance to recombination can be obtained by considering the ratio of the possible gene combinations in the F_1 to random combination. With three pairs of differing loci, $\frac{abc}{ABC}$, there can be a cross-over between the "a" locus and the "b" locus and between the "b" and the "c." Each of these will permit two recombinations, *viz.*, aBC, Abc; and abC, ABc. The total number of recombinations will therefore be equal to twice the number of gene abutments or $2(n-1)$ where "n" equals the number of differing gene pairs. With the two original com-

binations the total number of kinds of gametes will be $2n$. Since the total number of possible combinations, were it not for the restrictions imposed by linkage, is given by 2^n , the ratio we are seeking will be $2n/2^n$. For three pairs of gene differences this becomes $3/4$; for four pairs $\frac{1}{2}$; for ten pairs $10/512$, or less than 2 per cent.

Since the same principle will be operating in every cross-over region (tempered only by the occurrence of multiple crossing-over) the total hindrance in the entire germ-plasm will be enormous. An estimate can be obtained by considering the not impossible case of an organism which regularly has a single chiasma in each chromosome. For such an organism the ratio of the possible kinds of gametes to the total number of recombinations will be $\left(\frac{2n}{2^n}\right)^N$

where " n " equals the numbers of differing loci per chromosome and " N " is the number of pairs of chromosomes. For even such a slight difference as four genes per chromosome and with only six pairs of chromosomes this ratio becomes $1/64$. For ten gene differences per chromosome and with ten pairs of chromosomes it becomes $(10/512)^{10}$ or roughly less than one in 100,000,000,000,000.

It should be emphasized that this restriction is independent of the size of the F_2 and constitutes an absolute *upper* limit to gene recombination in that generation. The ratio $(10/512)^{10}$, inconceivably small though it may be, represents the fraction of the total combinations which could be achieved in a population of infinite size. In any actual F_2 the additional restrictions of combination frequencies will reduce the actual gene combinations to a fraction of this infinitesimal fraction.

It may therefore be predicted that linkage alone will greatly hinder recombination in species crosses, or in any cross where there is a considerable number of genes involved. Even with small numbers of gene differences in each cross-over segment, the possible recombinations among the gametes of the F_1 will be only a fraction of the total imaginable combinations. With any considerable number of gene differences the possible combinations will be only an infinitesimal fraction of the total combinations, and numerous hybrid generations will be required before there can be anything like complete recombination of those gene differences which have survived. These theoretical considerations suggest that the con-

ditions in the hybrid populations which have been studied are general phenomena.

EDGAR ANDERSON

MISSOURI BOTANICAL GARDEN
WASHINGTON UNIVERSITY

LITERATURE CITED

- Anderson, Edgar
1936. *Ann. Mo. Bot. Gard.*, 23: 511-525.
Anderson, Edgar and Leslie Hubricht
1938. *Am. Jour. Bot.*, 25: 396-402.
Anderson, Edgar and W. B. Turrill
1938. *New Phytol.*, 37: 160-172.
Delisle, A. L.
1937. *Gen. Prog. A. A. A. S.*, 101 meet., p. 121.
Goodwin, R. H.
1937. *Am. Jour. Bot.*, 24: 425-432.
Jones, D. F.
1920. *Jour. Am. Soc. Agron.*, 12: 77-100.
Riley, H. P.
1938. *Amer. Jour. Bot.*, 25: 727-738.

CHANGE IN GASTRIC DIGESTION OF KINGFISHERS WITH DEVELOPMENT

DURING our studies of the belted kingfisher (*Megasceryle alcyon*) in its relation to salmon (*S. salar*) and trout (*Salvelinus fontinalis*) we have had opportunities of making some observations on the digestion of fish by this bird.

The kingfisher has no crop. The proventriculus is not developed to the extent that it is in many birds. The muscles of the gizzard are thin and apparently unfitted for performing any vigorous grinding action. The gizzard, being thin walled and distensible, is not unlike the stomach of carnivorous mammals. The intestine has a small lumen and is long and symmetrically coiled above the gizzard (intestine of young kingfisher 6.8 times length of bird).

DIGESTION IN NESTLING

We have reared several young kingfishers and have examined the stomach contents of nestlings which had been preserved in formalin. The young will consume daily from one to one and three quarter times their weight in fish. Before the development of the flight feathers, *i.e.*, until they are about a month old, the young birds will digest all the bones and scales of the ingested

fishes (even when fed artificially on bony pieces of large adult fishes). While making food analyses of nestlings which had been collected from the nests, we were able to verify the observations made on the reared birds. The stomachs showed bones in various stages of digestion, and in some instances all the fish bones had been dissolved with some of the flesh still undigested. There was some softening of the chitinous parts of insects, but considerable quantities, from the food of digested fishes, had accumulated in their stomachs. When washing the stomach contents of the nestlings, even when there was little trace of other fish remains, there was generally considerable free fish oil floating on the water.

DIGESTION IN FULLY FLEDGED BIRDS

A short time before the complete development of the flight feathers the young, as found during rearing, began to disgorge stomach pellets of partly digested fish bones. By the time the young are sufficiently fledged to leave the nest, digestion of bones has ceased and thereafter they disgorge the complete skeletons, even of very young fishes, as well as the larger scales of the fishes which they have eaten. Large numbers of bone pellets may be found along streams beneath kingfishers' perches. We have used these pellets in our studies of the food of the kingfisher. The bones are well cleaned without breaking, there is no erosion or absorption and they make excellent material for the identification of the species of fishes captured by the birds. The larger scales are equally well cleaned and we have used them for age determination of the fishes. The chitinous parts of the insects from the stomachs of ingested fishes are disgorged with the bones.

For the purpose of food analysis many fully fledged kingfishers (adults and juveniles) were shot and preserved in formalin. When these were examined it was found that the condition of the stomach contents confirmed the observations made on the pellets. The food showed no evidence of any grinding and in many of the stomachs, pellets were found in various stages of formation. When washing the contents there was seldom even a trace of free fish oil on the water.

Observations on the reared birds showed that during their development they disgorged no pellets until near the time when they became fully fledged. The examination of the stomach contents of nestlings and fully fledged birds has shown in the former all stages in the dissolution of bones and scales, a slow softening

of chitin and no saponification of fish oil, whereas the latter have shown no digestion of bones, fish scales or chitin but a rapid saponification of fish oil.

These observations indicate a change from an acid reaction in the stomachs of the nestlings to an alkaline reaction in the stomachs of the fully fledged birds.

H. C. WHITE

FISHERIES RESEARCH BOARD OF CANADA

PRELIMINARY EXPERIMENTS ON THE COLOR
CHANGES OF *ANOLIS CAROLINENSIS*
(CUVIER)¹

No one can observe the American chameleon, *Anolis carolinensis* (Cuvier), in a garden, yard or field without being impressed by the readiness with which it changes in color from brown to green and *vice versa*. Because its life is largely spent in an environment of green and brown the phenomenon of metachrosis is attributed to the function of protective coloration. However, under continued observation the chameleons are frequently seen to be green on a brown background or brown on a green background. These observations suggest the possibility that the American chameleon reacts to the quality as well as to the intensity of light. Light perception, either qualitative or quantitative, to bring about bodily changes in color must be through photoreceptors (the eyes, parietal eye or receptors in the skin) or by direct action of light rays on the chromatophores in the skin. It is well known that in darkness these lizards turn green. No references mention a reaction to any of the colors of the spectrum.

To clarify the sometimes confusing observations on the color changes in the field, chameleons were collected during April and May, 1938, and the following experiments carried out under laboratory conditions.

- (1) Brown and green individuals were placed in darkness.

Result: All animals became green.

- (2) Brown individuals were placed in a glass jar covered with green Cellophane and exposed to light, either daylight or artificial light.

Result: Chameleons turned green.

- (3) A green hood of Cellophane was fastened over both eyes and the parietal eye; and these specimens were then exposed to daylight or artificial light.

¹ The writer is deeply indebted to Dr. L. H. Kleinholz, of Harvard University, for encouragement and for criticisms of the manuscript.

Result: Turned green or stayed green as long as the green hoods were kept in position.

- (4) Green hoods were placed over both eyes and a black patch was fastened over the parietal eye and the individuals were exposed to daylight or artificial light.

Result: The same as in 3.

- (5) Black patch over parietal eye only and the individuals exposed to daylight or artificial light.

Result: Same color reactions as shown by the specimens with no eyes covered.

- (6) A black hood was placed over both eyes and the individuals exposed to light, either daylight or artificial.

Result: All specimens turned a deep chestnut brown in sharp contrast to other chameleons in the cage whose eyes were uncovered and which were yellowish brown in color.

- (7) A black hood was placed over both eyes and the parietal eye and these specimens exposed to daylight or artificial light.

Result: Same as in 6.

- (8) A black patch was fastened over one eye and a green hood over the other eye and these specimens then exposed to daylight or artificial light.

Result: Same color reactions as when both eyes were covered with green Cellophane.

- (9) Chameleons as described in 6 and 7 were placed in a glass jar, covered with green Cellophane and exposed to daylight or artificial light.

Result: Stay deep chestnut brown in color.

DISCUSSION

These experiments indicate that the parietal eye plays no part in light perception for color changes. Parker (1938) reached a similar conclusion in his study of *Phrynosoma*.

The light passing through the green Cellophane and then into the eyes brings about the green phase. This result was duplicated many times. Lizards with the green hoods were kept in a wire cage for as long as four days with unhooded chameleons as controls: the unhooded animals were consistently yellow-brown during the daytime. Individuals with the black hoods over their eyes turned a deep chestnut brown when kept in the same wire cage with the green-hooded chameleons and their controls. The differences between the three groups were striking and conspicuous. During the experiments one individual fitted with a green hood turned a deep chestnut brown when placed in the cage. Examination showed that the green hood had been applied so tightly that the eyelids of this animal were held in the closed position. When the green hood was loosened and the chameleon again placed in the

cage, it turned green and stayed green as long as the hood was kept on. A few chameleons with green hoods or in glass jars covered with green Cellophane appeared yellowish-brown instead of the expected green. When they were watched carefully, it was noticed that they were rather sluggish and were alternately closing and opening their eyes for short intervals. They were thus between the green phase to be expected as the result of the green hoods and the deep chestnut brown phase expected of those individuals whose eyelids were closed for long periods of time with the body exposed to light.

The above experiments check with the writer's observations of chameleons in the field. In conditions where green leaves serve as a heavy green screen over the chameleons, they are green, regardless of background. The writer has watched green chameleons climb from under dense green foliage so that they were exposed directly to the sky light. These individuals then turned brown and were very conspicuous against the green background.

SUMMARY

Light, even after passing through green Cellophane, acts on the body alone (not through the eyes) causing a dark brown chestnut phase (extreme expansion of the chromatophores).

Light passing through a green Cellophane filter into the eyes inhibits the expansion of the chromatophores or causes their contraction so that the chameleon is green. Intermediate shades are the result of differing proportions of green light coming into the eyes, determining the extent of chromatophore inhibition.

Absence of light entering the eyes and the absence of light on the body also inhibits the expansion or causes the contraction of the chromatophores.

Green light can stimulate the retinal receptors to effect the green coloration but is not an effective stimulus for dermal photoreceptors or the chromatophores which can not perceive changes in the quality of the stimulus.

F. H. WILSON

DEPARTMENT OF ZOOLOGY,
TULANE UNIVERSITY OF LOUISIANA

LITERATURE CITED

- Parker, G. H.
1938. *Jour. Exp. Biol.*, 15: 48-73.

